FORAMINIFERA OF THE UPPER LIMESTONE GROUP OF THE SCOTTISH CARBONIFEROUS.

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C O N T E N T S.

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INTRODUCTION.

The earliest research on Scottish Carboniferous foraminifers was carried out by Brady almost a century ago. He identified two species recorded from two localities in the Upper Limestone Group in the faunal lists of Young & Armstrong (1871) and, later, with the aid of the Geological Survey collectors, through the services of Etheridge, the Survey palæontologist at that time, produced a list of nine species from four localities (Brady 1873). In 1876 Brady's monograph was published embodying the results of the study of material obtained largely from the Geological Survey. Sixteen species were recognized from nineteen localities which covered the range of the more important limestones in the Upper Limestone Group. Recently Cummings (1955a, 1955b, 1956) restudied Brady's collections and the material in the collections of the Geological Survey, and made important revision of the taxonomy. Otherwise, no particular study has hitherto been made of the foraminifers from the Upper Limestone Group, and despite the works cited, not a great deal is known about their distribution or stratigraphic significance.

Stratigraphy:

The Upper Limestone Group is the uppermost division of the Scottish Carboniferous Limestone

Series and, together with the lower part of the overlying Passage Group, is of Upper Eumorphoceras (E_2) age (Currie, 1954, p.535). Its position in relation to the Carboniferous strata elsewhere is illustrated in Table 1.

Table 1.

SCOTLAND	ENGLAND	
Coal Measures	Coal Measures	Westphalian
Passage Group		
Upper Limestone Group	Millstone Grit Series	Namurian
Limestone Coal Group		
Lower Limestone Group	Carboniferous Limestone Series	Visean
Calciferous Sandstone Measures		

The sediments of the Upper Limestone Group display a rhythmic sequence but tend to be predominantly arenaceous with thin limestones and coals, in contrast to the thick coals and paucity of limestones of the Limestone Coal Group, and the thick limestone shale sequences of the Lower Limestone Group. The limestones, however, although often poorly developed and argillaceous, are persistent and enjoy a wide lateral

development with the major horizons present throughout the Midland Valley of Scotland. A number of minor limestones occur which are of much more limited extent, but whose stratigraphic position can often be widely recognised as they pass laterally into poorly fossil-:iferous shales and sandstones. The succession of limestones is as follows, with the top and bottom of the group defined by the Castlecary and Index Limestones respectively:

Major Limestone	Minor Limestone
Castlecary	
	Plean No.3
	Plean No.2
	Plean No.1
Calmy	
	Myremailing Marine Band
Orchard	
Lyoncross	
	Huntershill Marine Band
Index	

The foraminifers are, of course, confined almost entirely to the marine limestone and calcareous shale phases of the sedimentary cycle. In Table 2 some indication is given of the distribution and thickness of the marine horizons within the Midland Valley.

The stratigraphical interpretation followed is broadly that of the Scottish Geological Survey in

TABLE No.1.
Variation in the thickness of the Upper Limestone Group and its marine horizons

	Bowhill No.12 Bore	Beach Bore	New Cumnock Collieries	Carbellow no.87 Bore	Linthouse No.3A Bore	Lugton Water, Montgreenan	Caaf Water, Dalry	Wolfcrooks No.1 Bore	Brokencrossmuir No.1A Bore	Watstonmids No.1 Bore	Hartwood Bore	Queenslie No.2 Bore	Cardowan No.3 Shaft	Rosehill No.1 Bore	Mossneuk Bore	Culross Bore & Blair Mains No.2 Bore	Boreland Bore	Monkton House Bore
Castlecary Limestone	www	www	www	www	www	www	www	www	www	www	www	www	www	www	8	8	8	12
Plean No.3 "	www	www	www	www	www	www	www	www	www	www	www	www	www	s.w.f.	s.w.f.	s.w.f.	www	L
Plean No.2 "	www	www	www	www	www	www	www	www	www	www	1	www	www	1	1	s.	www	0.5
Plean No.1 "	www	14	www	www	www	www	2	7	2	4	1	3	1	2	1	s.	s.	0
Calmy "	www	50	40	24	20	www	38	13	7	5	7	5	5	6	7	3	3	3
Myremailing Marine Band	www	0	0	0	0	www	0	s.w.f.	s.w.f.	0	0	3	3	0	s.w.f.	s.w.f.	0	0
Orchard Limestone	10	s.	3	4	s.	3	20	4	4	2	2	1	1	1	1	1	0.5	4
Lyoncross "	s.w.f.	0	0	6	0	3	4	5	2	s.w.f.	2	1	1	0.5	0.5	s.w.f.	0	s.w.f.
Huntershill Marine Band	0	0	0	0.25	0	0	0	sd. l.	0	s.w.f.	1	1	s.w.f.	0	s.w.f.	s.w.f.	0	0
Index Limestone	10	7	10	7	9	6	12	8	7	fault	4	5	7	3	3	5	s.w.f.	3
Total Thickness (feet)	98	178	135	420	140	85	366	528	276	482	644	862	888	1,410	1,278	1,770	1,110	882

www unconformity s.w.f. shale with marine fossils s. shale L shale with Lingula sd. l. sandy limestone

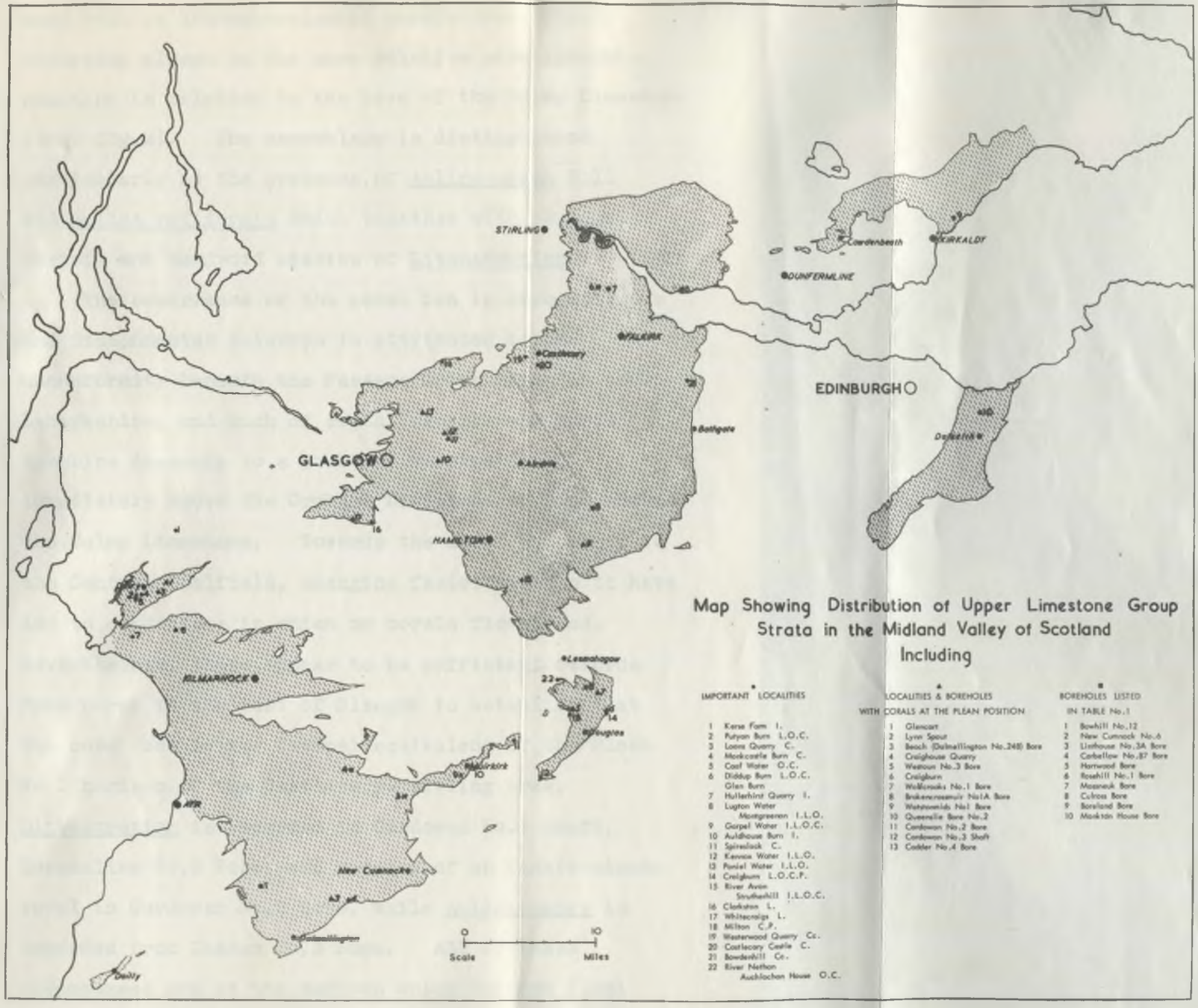
Memoirs dealing with the economic geology of the various coalfields, but differs in the interpretation of the stratigraphy of the Calmy and Plean No.1 Limestones in Ayrshire and South Lanarkshire.

The Plean No.1 Limestone was first encountered in boreholes in the Castlecary-Stirling area of the Central Coalfield (Crampton, 1917, pp.21-22, 37-41) and the characteristic succession of this area can readily be recognized throughout Stirlingshire, Clackmannan and West Fife (Dinham, 1932, pp.96-124, Francis, 1956 and Read, 1959, pp.31-38). Outwith this area the succession is broken by a number of minor unconformities, and the Plean limestones were not recognized in the western part of the Central Coalfield until recently, having been confused with the Castlecary Limestone or marine bands within the Passage Group. Forsyth (1961, pp.219-224) demonstrated the presence of the Plean Limestones in the east of Glasgow and the similarity of the succession to that in the type of area. Further evidence from boreholes and outcrops suggests that these correlations can be extended to Ayrshire and South Lanarkshire, although the interpretation is complicated by lateral changes of facies and the extensive unconformity of the base of the Passage Group.

A characteristic feature of the limestones of the Upper Limestone Group is their almost complete

TEXT - FIGURE 1.

Map showing the distribution of Upper Limestone Group strata in the Midland Valley of Scotland, and showing the distribution of important localities from which abundant foraminifers have been obtained. The limestones outcropping at these localities are indicated by their initial capital letters, i.e. I, Index - Cc. Castlecary.



Map Showing Distribution of Upper Limestone Group Strata in the Midland Valley of Scotland Including

● IMPORTANT LOCALITIES

1 Kerse Farm I.
2 Putyan Burn L.O.C.
3 Loans Quarry C.
4 Monkcastle Burn C.
5 Coal Water O.C.
6 Diddup Burn L.O.C.
Glen Burn
7 Hullerhirst Quarry I.
8 Lugton Water
Montgreenan I.L.O.
9 Glorpel Water I.L.O.C.
10 Auldhouse Burn I.
11 Spireslack C.
12 Kennox Water I.L.O.
13 Poniel Water I.L.O.
14 Craigburn L.O.C.F.
15 River Avon
Struthehill I.L.O.C.
16 Clarkston L.
17 Whitecraigs L.
18 Milton C.P.
19 Westerwood Quarry Cc.
20 Castlecary Castle C.
21 Bowdenhill Cc.
22 River Nethon
Auchlochan House O.C.

▲ LOCALITIES & BOREHOLES WITH CORALS AT THE PLEAN POSITION

1 Glencart
2 Lynn Spout
3 Beoch (Dalmellington No.248) Bore
4 Craighouse Quarry
5 Weenoun No.3 Bore
6 Craigburn
7 Wellcrooks No.1 Bore
8 Brakencraigmuir No1A Bore
9 Whitrowmlds No1 Bore
10 Queenslie Bore No.2
11 Cardowan No.2 Bore
12 Cardowan No.3 Shaft
13 Cadder No.4 Bore

■ BOREHOLES LISTED IN TABLE No.1

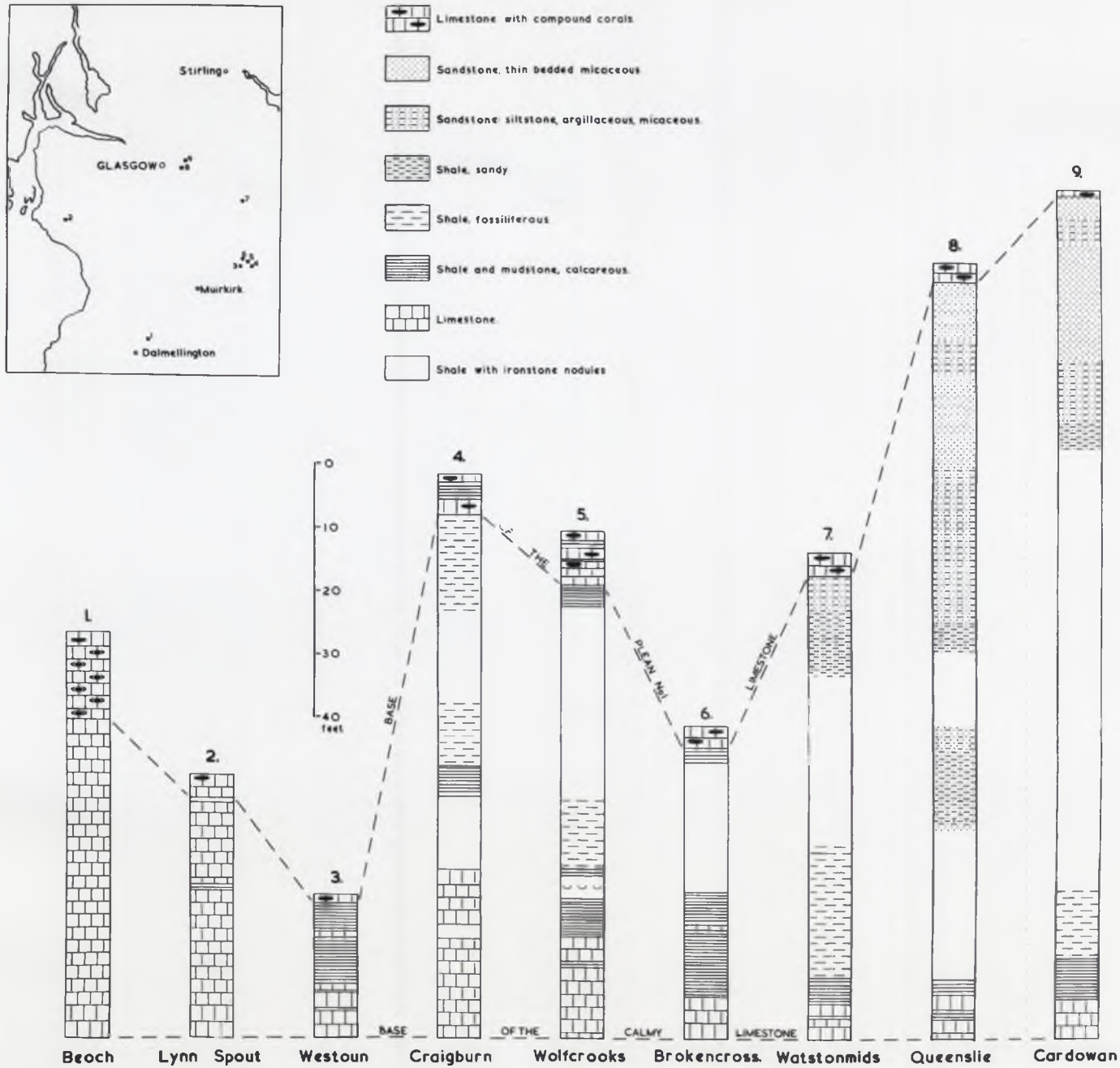
1 Bowhill No.12
2 New Cumnock No.6
3 Linthouse No.3A Bore
4 Corbellow No.87 Bore
5 Hartwood Bore
6 Rosehill No.1 Bore
7 Mossneuk Bore
8 Coltross Bore
9 Boreland Bore
10 Monkton House Bore

lack of compound corals. The single exception is a band rich in lithostrotiontid corals (text fig.1) occurring always in the same relative stratigraphic position in relation to the base of the Calmy Limestone (text fig.2). The assemblage is distinguished particularly by the presence of Aulina senex Hill and Aulina rotiformis Smith together with abundant cerioid and dendroid species of Lithostrotion.

The occurrence of the coral bed in discontinuous and disconnected outcrops is attributed to the unconformity beneath the Passage Group which in south Lanarkshire, and much of south, central and north Ayrshire descends to a position varying from immediately above the Orchard Limestone to just above the Calmy Limestone. Towards the north and east, in the Central Coalfield, changing facies appears to have led to conditions in which no corals flourished. Nevertheless, there appear to be sufficient records from bores to the east of Glasgow to establish that the coral bed is the lateral equivalent of the Plean No.1 horizon of the Castlecary-Stirling area. Lithostrotion is recorded in Cardowan No.3 shaft, Queenslies No.2 Bore, and nodules of an indeterminate coral in Cardowan No.2 Bore, while Aulina senex is recorded from Cadder No.3 Bore. All of these occurrences are at the horizon which Forsyth (1961 pp.219-224) established as the Plean No.1 Limestone.

TEXT - FIGURE 2.

The position of the coral bed in relation to the base of the Calmy Limestone, bringing out the lateral facies change in strata between Plean No.1 Limestone and the Calmy Limestone from Ayrahire (1,2) and South Lanarkshire (3-6), to the Central Coalfield (7, 8 and 9).


Stirling
GLASGOW
Muirkirk
Dalmellington
Limestone with compound corals
Sandstone, thin bedded micaceous
Sandstone, siltstone, argillaceous, micaceous
Shale, sandy
Shale, fossiliferous
Shale and mudstone, calcareous
Limestone
Shale with ironstone nodules
0
10
20
30
40
feet
BASE OF THE CALMY LIMESTONE
PLEAN No1 LIMESTONE
1
2
3
4
5
6
7
8
9
Beoch
Lynn Spout
Westoun
Craigburn
Wolfcrooks
Brokencross
Watstonmids
Queenslie
Cardowan

Unfortunately, the importance of the corals was not appreciated at the time that these bores were sunk, and thus material was not very thoroughly collected. Moreover, much of it was so severely recrystallized as to be considered indeterminate. However, despite the rather unsatisfactory condition of the recorded list of corals, it provides sufficient evidence to establish the equivalence of the Plean No.1 with the coral development in Ayrshire and south Lanarkshire.

In the vicinity of Dalry the sandstones of the Passage Group rest unconformably on the Calmy Limestone, and transgress that limestone as the Dusk Water Fault is approached. At Montgreenan, near Kilwinning where an almost complete section is to be seen in Lugton Water, two thin limestones occurring above the Index Limestone were tentatively referred to the Calmy and Orchard positions by Richey, Wilson and Anderson (1925 p.35). The foraminiferal assemblages demonstrate conclusively that the beds are the Lyoncross and Orchard Limestones. Thus the sandstones of the Passage Group transgress to a position immediately above the Orchard Limestone to the south of the Dusk Water Fault, and may step down further in central Ayrshire in the vicinity of the Inchgottrick Fault. A parallel occurs to the east in the southern part of the Central Coalfield where the Passage Group sandstones transgress from a position just above the Calmy Limestone down to the

Orchard Limestone in the vicinity of Larkhall and Stonehouse. The pattern of the unconformity beneath the Passage Group in north Ayrshire is repeated in south Ayrshire from the Inchgottrick fault south across the Kerse Loch Fault into the Dalmellington basin where the Passage Group rests just above the Plean No.1 limestone at Beoch Bore. Further to the east in Craighouse quarry the sandstones of the Passage Group can be seen with a conglomeratic base resting on the coral beds of the Plean position, while in New Cumnock No.6 Bore the base of the sandstones lies at a position below the Plean horizon but above the Calmy Limestone. It should be noted that on this interpretation of the stratigraphy of the Dalmellington basin the thickness of the Upper Limestone Group diminishes from over 1,000 feet to a mere 120 feet and, consequently, the change in thickness across the Kerse Loch Fault is only 30 feet, which may be explained simply by thinning of the strata northwards, and without recourse to contemperaneous movements on the Kerse Loch Fault.

Scope of Collection:

Material has been collected from practically every known locality in the Midland Valley, about 155 in all, and in addition, a small amount of material has been obtained from deep boreholes by the courtesy of the National Coal Board. At each locality the thickness and lithology of all the sediments associated with the

limestones were recorded and samples were collected from the limestones at approximately six inch intervals yielding a collection of 1,250 specimens.

At least 70% of the specimens collected have had their foraminiferal fauna obliterated through recrystallisation and replacement. As a result very little material has been obtained from the eastern part of the Midland Valley, and although there is a gradual improvement in preservation towards the west, nevertheless, limestones in which the fauna is preserved are the exception (Text fig.1).

Acknowledgements:

Grateful acknowledgement is made to the Coal Board for permission to examine records of boreholes and for access to material from a number of bores; to Dr. C.G. Adams for making available material from Brady's collection of Carboniferous and Permian foraminifers housed in the British Museum (Natural History); to Dr. W.D.I. Rolfe for material from the John Young collection in the Hunterian Museum of the University of Glasgow; and to Mr. D. McLean for invaluable assistance with photography.

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CHAPTER 2

A New Technique for the Study of Smaller Foraminifera in Indurated Limestone.

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INTRODUCTION.

In the past Upper Palæozoic small foraminifers have been studied by the identification of species and the application of their ranges to stratigraphy in the conventional manner applied to most Mezozoic and Tertiary foraminifers. The earliest workers, typified by Brady (1876), worked mainly with free specimens obtained from shaly or unindurated horizons, and this tradition was continued by such workers as Cushman, Waters, Harlton and Warthin in the American Pennsylvanian. Little or no attempt was made to study the internal structure of the foraminifers or to examine the nature and the effects of diagenesis upon it (Cummings 1955 and 1956). Furthermore, in many instances, there was a complete failure to recognise the effects of deformation and compaction in foraminiferal assemblages obtained from shales or shaly limestones.

In later work, particularly that of the Russians, partially in an extension of the methods employed on the fusulinids, the practice has been to diagnose and describe species from the abundant random fragments as seen in thin section. This process tends to be extremely arbitrary since the species is generally described on the basis of a single fragment which may reveal imperfectly the morphological condition of its biocharacters. Typically fragments in which

diagnostic specific characters may be recognized are scarce and imperfect and, as a result, little or no appreciation can be had of the variation of the species population. Indeed, there is the probability that fragments which are not typical of population will be described. The practice of describing forms in relation to one or two diagnostic planes of section frequently leads to misinterpretations of the three dimensional morphology and, clearly, if the structure of the foraminifer is not fully appreciated, errors are likely to arise in the inference of fragments to any particular species.

There is, therefore, a necessity for a technique which will enable a more precise analysis of the foraminiferal assemblages from indurated limestones. Thin sections are, of course, most useful, if not necessary, in providing a means of examining wall structures and the effects of diagenesis on the fauna; and in assessing the quantitative distribution of families and genera at any particular horizon, but they are generally inadequate for the study of morphology for systematic and taxonomic purposes.

Techniques are available for the maceration of indurated limestones, such as those of Kirchner (1958), Bolli (1950 & 1952) and Hussey & Campbell (1951) etc., but they are usually time consuming and the recovery of specimens is poor and biased in favour of foraminifers

of particular structural types.

Where indurated limestones are associated with more friable argillaceous beds, or calcareous shales, it may be possible to obtain free specimens for morphological study, but the foraminifers are often distorted from compaction, and the assemblage from the shale may differ markedly from that in the limestone both in numbers, and in genera and species represented. Moreover, hand picking of material is tedious even where concentration techniques are employed such as that suggested by Eichert and others (1961).

Even where material has been obtained from shale or limestone by maceration it is still necessary to produce orientated sections fully to assess morphology. Excellent techniques are, of course, available for this procedure. (Arnold, 1958, Van Morkhoven, 1958 and Pessagno, 1960). However, because of the inconveniences of the conventional procedures and the occurrence within the Upper Palæozoic rocks of many thick continuous sequences of indurated limestone, the following technique may fill the need for a means, other than thin sections, of studying small foraminifers in indurated limestones.

PROCEDURE.

Hand specimens, in which the presence of foraminifers has been confirmed by examining a slice flooded with oil of cloves, are cut, and the slices,

3-5 mm. thick, smoothed off with carborundum of the 600 grade. A coat of good quality clear varnish is then applied. The slices may now be examined for foraminifers and, conveniently, sections of interest may be marked with waterproof inks of different colcours for the various genera. Observation in this manner is normally satisfactory even where foraminifers prove to be very poorly preserved in thin section. Indeed, in many cases, examination of the foraminifers in rock slices has the advantage that it provides the third dimension which is lacking in thin sections. The clarity with which specimens can be observed varies, however, depending on the lithology and the degree of recrystallisation of the host sediment. Viewing of individual specimens can be improved by removing the varnish and covering the surface with a clearing agent such as nitro-benzene or clove oil which, if the infilling of the test is suitable, allows the interior of the test to be viewed in three dimensions. It will be obvious that the area observed in a series of slices of this nature is very much greater than that seen in thin sections, and, in consequence, many more fragments in axial or sagittal orientations are found. At this stage, thin sections, which are necessary to obtain the fullest information regarding the wall structure, the lithology of the limestone, and the diagenetic history, can be selected from slices which will give

the maximum amount of information.

Orientated sections of individual foraminifers are produced by paring down the specimen with a surgical scalpel to its axial or sagittal plane of section, which, for convenient working, should lie within 45 degrees of the surface of the slice. The position of each cut can be checked by irrigating the specimen with clove oil, and it is possible to adjust the angle of the cut as the specimen becomes increasingly exposed. The successive series of sections observed in this way provides a clear impression of the tests internal organization, and provides an excellent opportunity to relate random two-dimensional sections to the complete structure.

Scalpels with removable blades are most suitable for this procedure for they allow worn blades to be changed, and the shape and type of blade to be altered to suit the operator or the specimen. A single blade should last through a considerable number of sections, and its life may be extended by simply snapping off the worn or serrated tip with a pair of forceps.

Attempts have been made to produce sections by using miniature diamond discs coupled to a dental drill, but this equipment proved to be too cumbersome and difficult to control for work on small foraminifers. It is possible that it might be successfully used in the sectioning of larger

foraminifers in rock slices.

When the orientated section of the specimen is complete, its dimensions may be recorded with any other data that may be required. The number of orientated sections obtained is limited only by the area searched, and so more representative fauna can usually be found, including rare species, which would not be detected by conventional methods.

A comparison of rock slices and thin sections is given below.

Genera Examined	No. Orientated Sections: Area of Rock Slices 800sq.cm.	No. Orientated Sections: Area of Slides 900sq.cm.	Density of Fauna (37fragments/sq.cm. average density)
Endothyra	43 plus	7	3.4/sq.cm.
Paramillerella	36 plus	6	2.7/sq.cm.
Palæotextulariids	9	1	0.6/sq.cm.
Endothyranopsis	14	-	0,2/sq.cm.
Bradyina	6	1	0.15/sq.cm.

It is thus possible to obtain quantitative assessment of the variability of the populations of the assemblage and, therefore, more accurate systematic work is possible. Tests whose growth is not symmetrical about a single plane or axis, such as Climaccammina, Calcivertella, or Calcitornella, can be successfully examined.

It is possible to photograph the specimen in the slice by reflected light, but good results depend on the contrast between the wall of the specimen and its matrix. Nevertheless, even in poor conditions it is possible to obtain an outline which is useful for comparison and record purposes.

Finally, thin sections are prepared by coring the selected specimen from its slice, with a minimum of excess limestone, by means of a diamond impregnated hollow glass bit, commonly used for boring plate glass or mirrors, and available in a wide range of diameters. A flow of lubricant is normally required through the shaft of the bit, but it is probable that the bits could be adapted for use in an ordinary bench drill, for the demands made on them in cutting a few millimetres are not great.

On removal from the limestone the core is mounted on a slide in a thermoplastic cement such as Lakeside or Canada Balsam, and it is arranged in such a way that the plane of the orientated section is parallel to the slide. The excess limestone is then filed off by means of a 'frosted' glass slide, by the method outlined by Van Morkhoven (1958), which ensures that the excess material is removed parallel to the plane of section, and that the specimen itself is not damaged.

For a successful thin section it is essential that the surface prepared with the scalpel isflat.

This does not usually present any serious difficulty with small specimens (less than 1 mm.), but it can be troublesome with larger ones. If it is known that a thin section is required from a particular specimen it is often convenient to leave the section incomplete, to be ground down finally by the method suggested above. This ensures an absolutely flat finished surface ready to be remounted for the completion of the section.

By this method the foraminiferal assemblages can be thoroughly examined morphologically, and thin sections can be prepared from appropriate material, perfectly orientated, and displaying the typical characters of the populations. The technique has been used successfully in a study in which over one thousand sections were obtained for a single genus, and it is emphasised that, with a reasonable abundance of the material concerned, it is possible to cut 25-30 orientated sections in a day.

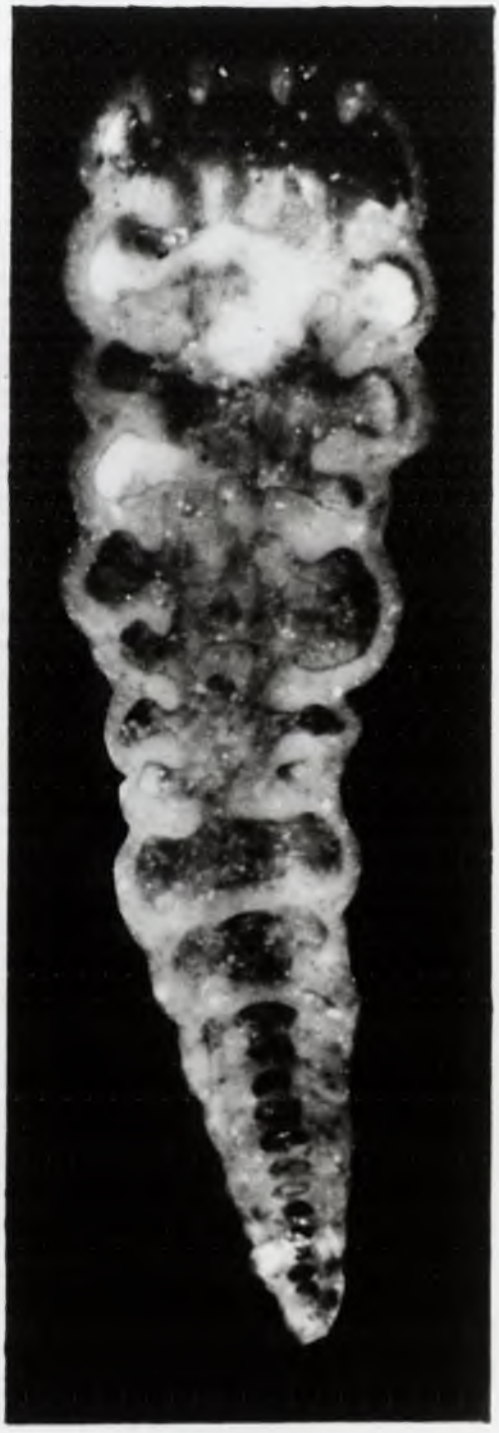
EXPLANATION OF PLATE 1.

1.2. *Climacammina antiqua* Brady, Lyoncross Limestone, Craigburn, Uddington, P.476:

1. a random section as it appears on the surface of a limestone slice. The three white ovals at the top of the photograph are sections tangential to the uniserial chambers of the specimen. X50.

2. the same specimen scraped down by means of a scalpel to its median plane of section in the plane of biserial overlap, showing eight pairs of biserially arranged chambers and eight uniserial chambers. X50.

1



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EXPLANATION OF PLATE 2.

1,2. Endothyranopsis sphaerica Rauser-Chernoussova Beljaev & Reitlinger, Plean Limestone, Beoch Bore, P.475/1:

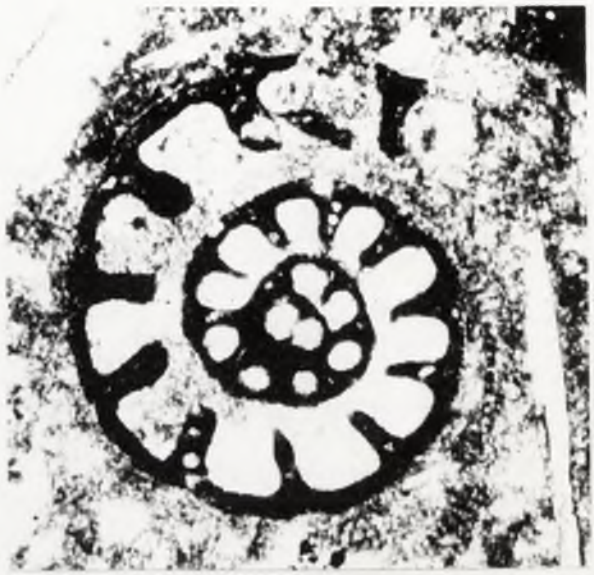
1. specimen on a core of limestone mounted in Lakeside cement prior to final sectioning. X17.
2. the completed section. X50.

3,4. Paramillerella craigburnensis sp. nov., Plean Limestone, Craigburn, Uddington, P.469/23:

3. axial section in reflected light, from section scraped down by means of a scalpel. X100.
4. the same specimen in thin section. X100. (transmitted light).

5. Paramillerella craigburnensis sp. nov., Plean Limestone, Craigburn, Uddington, P.469/26: sagittal section in reflected light from section on limestone plate. X100. During the scraping down of this specimen it was observed that damaged chambers in the last whorl had been repaired by three large irregular chambers. The last whorl originally had 21 chambers.

1



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CHAPTER 3.

Endothyra, *Paramillerella* and associated endothyrid and primitive fusulinid foraminifers.

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MORPHOLOGY.

The individual specimen can be considered analytically as the expression of a number of separate morphological units each displaying a particular condition. Each unit or biocharacter, however, must be considered within the context of the other biocharacters, and the series of change in the condition of a biocharacter analysed with a realisation of the limitations imposed on it by the adaptive demands of the interdependant biocharacters.

The morphology of endothyrid foraminifers can conveniently be reviewed in terms of the following biocharacters; the primary test wall; secondary deposits; chamber form and arrangement; septa; and aperture. (The term endothyrid is used here for the family Endothyridæ as defined hereunder, and it includes the primitive fusulinid foraminifers with a short axis of coiling.

The Wall.

This biocharacter is of fundamental importance in the classification of the super family Endothyracea, Glaessner (1945), and its structural development is used as a basis for major taxonomic categories as well as for generic distinctions. Wood (1949 p.239), has pointed out that compositionally, at least, the wall of the endothyrids and the fusulinids is identical, while a number of typically fusulinid wall structures

have been described among endothyrid foraminifers. It is, therefore, necessary to consider the character of the wall in both families.

A review of the literature shows that there is a strong tendency to describe the wall structure of the Endothyracea according to a conventional straitjacket which very often tends to obscure the true character of the wall, and which, descriptively, leaves much to be desired. The set terminology of upper and lower tectoria, tectum, and diaphanotheca particularly, appears to be inadequate, when these terms are used without any descriptive amplification, and it is obvious in many cases, that the same term is being used to describe layers of quite different character and origin. For example the wall of Millerella was described by Thompson, (1948, p.13 and 1964 pc.374, in Loeblich & Tappan 1964), as a tectum with upper and lower tectoria, although it is now clear (Skinner & Wilde 1954) that the lower tectoria, supposedly a secondary deposit, was really the primary wall. Similarly, Anisgard & Campau (1963 p.105) described the wall of a species they referred to Paramillerella as having an 'upper tectum'. This structure, on examination, proves to have a distribution which conclusively demonstrates that it is a secondary basal lining of the chambers, an upper tectoria. There is, in fact, no tectum in the normal sense of the term, a fact which these authors were obviously reluctant to

admit. In many ways the emphasis on the layering of the endothyrid wall appears to be exaggerated beyond its morphological significance. The true nature of some of the layers is ambiguous and they are, as a result, of doubtful taxonomic value.

Conventionally the wall of the fusulinids and, by extension, endothyrids, is considered to include the primary wall (protheca), and the secondary deposits (epitheca), but they may be conveniently considered as distinct biocharacters since they are not interdependant: one may show major changes in condition independant of the other.

The protheca is normally taken to consist of two layers; a thin dark film, the tectum, underlain by a thicker slightly more transparent layer in which the major structural changes of the endothyracean wall occur. The precise nature of the tectum is not clear and the usage of the term in the literature is not particularly objective. There is in many cases a tacit acceptance of tectum as any dark zone on the outer margin of the protheca, or between protheca and epitheca without any attempt to check its structural validity. Henbest (1937 p.317-320) has shown that the tectum is a feature of composite origin such as: the optical effect of constrictions at the outer end of keriothecal pores; a darker zone in the basal layers of epitheca in overlying volutions; and the optical illusion caused by two plane objects in imperfect

contact, which may be exaggerated by the discolouration of the protheca by impurities before the deposition of the epitheca. To this may be added the effects of diagenesis which by recrystallisation and replacement often introduces an apparent layering (Plates 3-5).

Henbest's findings have been ignored in most later generalizations and many authors, notably Skinner & Wilde (1954 p.227) and Dunbar (1963 p.29), appear to accept the fact that the tectum represents a homogeneous layer of the protheca which results from the differential distribution of organic matter according to the theory of Gubler (1935 p.13). As Wood (1949 p.240) has pointed out, Gubler's observations regarding the distribution of organic matter are suspect since he interpreted the inorganic crystalline infilling of the alveoli as original secretions consisting of coarse globulites of calcite cemented by a selvidge of tectine. In fact, Gubler, whose observations were based mainly on Pseudofusulina, found no differentiation of organic matter in the protheca for he considered the tectum and the walls of the alveoli identical in structure; thus confirming that the tectum is simply the zone of alveolar constriction in a wall of homogeneous composition.

Careful examination of the wall at high magnifications in general, fails to reveal any evidence of organic material, but shows that it is composed of homogeneous, very finely granular, calcite with no

preferred crystallographic orientation. When well preserved material is examined it usually proves virtually impossible to distinguish individual granules, even using oil immersion objectives with magnifications up to X 1000. This is because in the average thin section there are about 15-25 granules in the depth of the slide. Sometimes the protheca or epitheca may lie in the plane of the section and so be ground down to a very thin layer in which, with some difficulty, the individual crystals can be observed. The wall of Paramillerella then appears as a closely packed mass of rather rodlike or sometimes tabular crystals from 0.75 - 1.5 microns in length, and approximately 0.25 - 1.0 microns in width; a structure very similar to that described by Hay & others (1963) in parts of the wall of the porcellanea. Wood (1949 p.239) has already drawn attention to the similarity in the structure and appearance of the walls of the fusulinids and the porcellanea. If this comparison is accepted, then the studies of Hay, Towe & Wright clearly indicate that the wall itself contains no organic cement, and, therefore, the suggestion that the varying distribution of tectine is responsible for differences in the opacity of the wall must be rejected.

The residue of tectine recovered by Zeller (1950 p.4) from Plectogyra probably originated not as an intergranular sheath or cement, but as a thin intercameral layer; a

remnant of the organic sheath which appears to envelope the wall of a variety of genera as described by Hay & others (1963 pp.171-195). In fossils the organic sheath is preserved only in positions where it is enclosed between successive layers of the wall, and it is possible that the layer itself or the products of its decay will cause a dark zone in the intercameral suture, or between the epitheca and protheca.

It has been suggested by Wood (1949 p.239) that the opacity of the granular calcareous wall is due to the loss of light through reflection and internal refraction at the crystal interfaces, and a study of recrystallized material confirms that the wall becomes increasingly translucent with progressive grain growth. It has been observed that the opacity of the protheca tends to vary directly with its thickness, and this could logically be attributed to a change in the grain size with the thickness of the wall. It is not possible to confirm this observation microscopically because only a small area of wall can be observed at one time, while mensuration is not sufficiently accurate to provide meaningful comparison.

It is, therefore, conceivable that the tectum might result from a more finely granular zone on the outer margin of the wall, although a tectum, other than that resulting from optical or diagenetic effects, has not

been observed in the large number of endothyrids examined. It is possible that this could be accounted for by a widespread loss of the tectum due to recrystallisation. Wood (1949 p.239) thought that the wall of Endothyra, despite its uniform grain size, may not be in its original state because it is closely similar to the recrystallised wall of Alveolina or Alveolinella. He believed that there was a check on recrystallisation which prevented grain growth from proceeding beyond a certain stage, and this was tentatively attributed to the growth of the granules to fill the interspaces left by the organic matter which is presumed to have decayed during lithification. The check on grain size is in reality an optical effect which depends on the contrast in size between the grains of the wall and those of the matrix and test infilling. As grain growth proceeds the crystals in the wall increase in size and decrease in number, becoming increasingly transparent, until, at a certain stage, the grains become undistinguishable from the matrix. Thus, in most cases, the fact that the wall is distinct suggests that the grains are less than an optimum size of about 3 - 4 microns. Beyond this grain size the wall of the foraminifers tends to become transparent, and unless there is a marked contrast in grain size or colour between the wall and the matrix the foraminifers are not visible. (Plate 4

fig. 2-4 and Plate 7).

The protheca, therefore, can be considered as a compositionally constant biocharacter which is modified structurally in response to the loss of the aperture and the considerable expansion in test volume. The fundamental changes in the biocharacter are the consequence of progressive changes in the number, shape, and arrangement of the mural pores. The interplay of the inorganic infilling of the pores with the granular material of the wall results in the varying opacity observed in this section.

The tendency has been to regard the endothyrids imperforate, however, Skinner & Wilde (1954 Plate 49, fig.3) have figured a specimen of Millerella showing distinct pores picked out by an iron ore. Normally preserved endothyrids do not usually show any clear evidence of pores, but a careful investigation of the wall may reveal a few very fine transverse discontin-:uities in the form of thin bright or dark lines across the apparently homogeneous dark wall (Reitlinger 1950 p.8, Plate 1 fig.2, Igo 1957 p.158 and St. Jean 1957 p.18). Zeller (1950 p.5) argued that such structures were the result of crystal alignments possibly through recrystallisation, and it is possible that this explanation is the correct one in a number of cases. Examination of topotype material shows that the

fusulinellid structure of Plectogyra baileyi. described by Scott, Zeller & Zeller (1947 p.558) is a recrystallisation fabric which appears to be dependant upon the development of fibrous calcite in the oolitic facies in which these forms are found. In general, however, it is apparent that the transverse structures result from an interplay of the infilling of the pores with the granular wall. (Plate 6 fig.1-3).

Observation of material with distinct pores (Henbest 1937 and Skinner & Wilde 1954) shows that there is a close relationship between the thickness of the wall and the diameter of the pores. Commonly, the diameter of the pores is about one tenth of the thickness of the wall, and this relationship can be observed in individual specimens as the pores increase in diameter with increasing thickness of the protheca, both from the proloculum outwards, and from the poles into the tunnel. As the number and size of the pores increases, and thus the volume of more translucent coarsely granular pore infilling, so the wall becomes progressively less opaque. Therefore, in species such as Fusulinella fugax Thompson and Profusulinella primaeva Skinner, which have been regarded as having wall structure transitional from the profusulinellid to the fusulinellid condition, the diaphanotheca appears first in the outermost whorls over the tunnel, in the

zone of maximum pore development. Thus diaphanotheca is directly the result of the development of the mural pores and it is not due to changes in the amount of organic matter as has been suggested by Skinner & Wilde (1954 p.447) and Dunbar (1963 p.30). This progressive enlargement of the pores in the wall of the fusulinids is essentially paralleled during the ontogeny of certain species of Bradyina. In these the wall of the proloculum and the first chambers, is dark and apparently homogeneous, but, as the wall becomes thicker, it becomes lighter in colour and it passes through a pseudofibrous stage, (diaphanotheca) before the truly alveolar character of the wall can be recognised, (keriotheca). The alveoles in Bradyina constrict at their outermost extremity, and they connect with exterior only through very fine pores. Thus there is an outer, rather dark, thin layer which could be described as a tectum. This practice has not generally been followed in the literature, although from time to time the similarity has been commented on, notably by Henbest (1937 p.218) and St. Jean (1957 p.18).

Usually the fine granular wall of Endothyracea is quite resistant to the effects of recrystallisation through redistribution or replacement, but there are certain genera (Pseudoendothyra, Nankinella, Staffella, Eoverbeekina, and Sphaerulina.) whose wall seems

particularly prone to alteration. Indeed, this sensitivity is so great that these genera are mostly severely recrystallised or replaced while adjacent forms show quite normal preservation. (Plate 7 fig.2).

A number of authors (Rauser, 1948 p.14, Moeller, 1878 Rozovskaya, 1963 p.70) suggest that the wall is four-layered, consisting of tectum, diaphanotheca, and upper and lower tectoria. This would appear to be a conventional fiction arising from early descriptions of these forms where the role of secondary replacement was not recognised. As Thompson (1948 p.30) points out the wall is typically so altered that the fine structure cannot be determined, while there is also a tendency for the recrystallisation of the wall to induce a more strikingly layered appearance. Material studied of Pseudoendothyra suggests that the wall has a thick undifferentiated protheca, with thin secondary deposits confined mainly to the septal ends, and not reaching the roofs of the chambers or coating the floor of the chambers in the median zone of the test. There is nothing to suggest that the wall of Pseudoendothyra is different from that of Endostaffella or Paramillerella in its fundamental structure. Certainly the wall is thicker and the basal deposits thinner than equivalent specimens of subgenera Chernousovella, and Paramillerella, but the difference

in the behaviour of the walls suggests that the underlying difference is compositional rather than structural. The 'diaphanotheca' of Pseudoendothyra, results not from the increasing size of the pores as in the case of Profusulinella fugax and Fusulinella, but through recrystallisation of the original shell material of the protheca. The protheca of the staffellids may be more porous than the other fusulinacean genera but this cannot be the underlying cause of their typical recrystallisation and replacement.

The evidence suggests that the contrast in the behaviour of the two types of test might result from the presence of a primary aragonite wall in the staffellid forms. It is well known that aragonite is unstable and highly sensitive to solution and recrystallisation during diagenesis such that it is very rarely preserved in Carboniferous fossils. The inversion from aragonite to calcite is usually accompanied by some loss of detail in the shell structure and, in Carboniferous mollusc shells aragonite structures tend to be completely replaced by coarse clear calcite mozaics. Simon & Bell (1963 p.1179) have indicated that very finely crystalline aragonite is particularly subject to inversion so that complete loss of structure is to be expected if the original wall was finely granular. Wood (1949 p.39) considered the normal

recrystallisation of a fusulinid to be in complete contrast to that of a gastropod or an ammonite shell, but in the case of the staffelid wall the comparison is close. Since most gastropods and ammonites have a shell of aragonite the analogy may be appropriate. Todd & Blackman (1959 p.13) after a study of a large number of recent genera, concluded that:

a.) gross mineralogical nature of shell, that is whether it is calcite or aragonite, is a genetic characteristic in the foraminifers and is not determined by environment.

b.) among recent foraminifers aragonite tests seem to be restricted to the families Robertinidae and Ceratobuliminidae.

c.) no combination of aragonite with calcite occurs in foraminifers.

These findings suggest that the foraminifers with a staffellid wall should be considered as a separate family within the Endothyracea. This view is supported by the fact that the genera noted, although ranging from Middle Carboniferous to upper Permian, form a distinct group conservative in test morphology.

The use of a recrystallised wall as a systematic criterion is admittedly rather unsatisfactory but, nevertheless, appears to be justified, for, in the more advanced Middle and Upper Carboniferous and

Permian forms it is supported by distinctive morphological characters, and there is little ambiguity. But in the more primitive Lower Carboniferous forms the shell architecture is essentially homologous with that of Paramillerella, and here, undoubtedly, there is considerable ambiguity, for it is not certain that Pseudoendothyra would be recognised in an unaltered limestone, or conversely, Paramillerella in a strongly, but patchily, recrystallised limestone. The most primitive staffellid forms can be identified with certainty only in the presence of unaltered endothyrids or fusulinids, (Plate 7 fig.2) otherwise one cannot be certain that the clear wall resulted from greater diagenetic sensitivity.

Unfortunately, of the some 75 species of Pseudoendothyra described none give any satisfactory background regarding the nature of the host sediment and the associated fauna. Moreover, they are simply stated to have a clear wall or diaphanotheca with little or no qualification as to its origin. (Rauser 1948, Vissarionova 1948, Schlykova 1951, Durkina 1959, Grozdilova and Lebedeva 1950, 1954 and 1960 etc.). Clearly, 'diaphanotheca' is an unsatisfactory term in this context, and should be avoided in favour of a more detailed textural description of the wall. The term, diaphanotheca, is currently being used in three

different senses; the one discussed above; that of Thompson (1948 p.13) in Fusulinella; and that of Skinner & Wilde, (1954 p.447) and Igo (1956 p.158) in Profusulinella and Paramillerella.

Secondary Deposits (epitheca).

Secondary deposits are characteristically present in the Endothyracea, and their initial elaboration and changing morphological expression can be readily observed among the endothyrids. The function of this biocharacter would appear to have been twofold, in part to provide a reinforcement of the sutures of the test, and in part to channel and direct cytoplasmic flow. Three major conditions of this character can be recognised:

a.) Tests in which secondary deposits are confined to a thickening of the end of the septum at its suture with the previous whorl. These deposits very often do not cross the floor of the chambers, although they may become somewhat more extensive towards the poles of the test. (Pseudochomata).

b.) Tests in which the secondary deposits occur in sharp ridges or hooks parallel to the septa and are at their maximum expression in the final chamber.

c.) Tests in which the secondary deposits occur parallel to the tunnel in fairly uniform ridges but reaching their maximum expression at least half a whorl before the final chamber. (Chomata).

These broad types of secondary deposit appear to represent characteristic differences in cytoplasmic organisation and there would certainly appear to be justification for the view of Voloshinova & Reitlinger in Rauser-Chernoussova (1959 p.242) that the character of the basal deposits provides a basis for subfamilial or generic differentiation. The recognition of both hook like deposits and chomata in the same specimen by Anisgard & Campau (1963 p.99) is based on a misinterpretation of the structure, for none of their sections show chomata in the interseptal area. The deposits they describe do not appear to differ from the basal coating or connecting deposits normally associated with vestibular hooks or ridges.

It is important to recognise and describe in detail the distribution of the epitheca which can occur within the chamber in the following forms:

Floor epitheca - a fairly uniform layer on the base of the chamber.

Septal epitheca - a layer which may cover the septum in a uniform fashion,

but is commonly thickest on the posterior edge of the septum over the tunnel.

Roof epitheca - a layer which may be quite uniform, but is frequently thinner than the floor epitheca, and is often absent in the peripheral zone of the test over the tunnel.

The relatively evenly distributed epitheca described above is conventionally referred to as 'upper and lower tectoria', but it is emphasised that, as such, the tectoria should constitute layers unquestionably distinct from the primary wall, and not a vague dark zone on the edge of the protheca which might result from the alteration and decay of the organic lining of the wall, diagenetic or optical effects.

The more specialised epitheca occurs in the following conditions:

Chomata - levee like ridges parallel to the tunnel between the septa.

Sutural Deposits - wedge like deposits of epitheca occurring along chamber sutures and includes Pseudochomata - a thickening of the septal suture adjacent to the foramen.

Basal Deposits or Connecting Deposits - floor epitheca which thickens into the sides and poles of the chambers.

Vestibular Hooks and Ridges - ridges of epitheca situated behind and parallel to the aperture. They are often very prominent and strongly anteriorly directed with convex posterior and concave anterior surfaces.

Axial Deposits - epitheca filling the chamber completely at the poles.

The thickness of the epitheca does not appear to be influenced by the degree of resorption necessary to maintain the tunnel since the aperture is lost without producing any major change in the distribution or massiveness of the epitheca. How far the massiveness of the epitheca is related to ecological factors is not clear, but it may be a factor deserving consideration for it has been shown that the robustness and ornamentation of foraminiferal tests can be affected by salinity (Heron-Allen, 1914 p.227 & 1920 pp.163-177) and the nature of the host sediment, (Hendrix, 1958 p.649).

Petrographic investigation shows that the epitheca is composed of homogeneous finely granular calcite

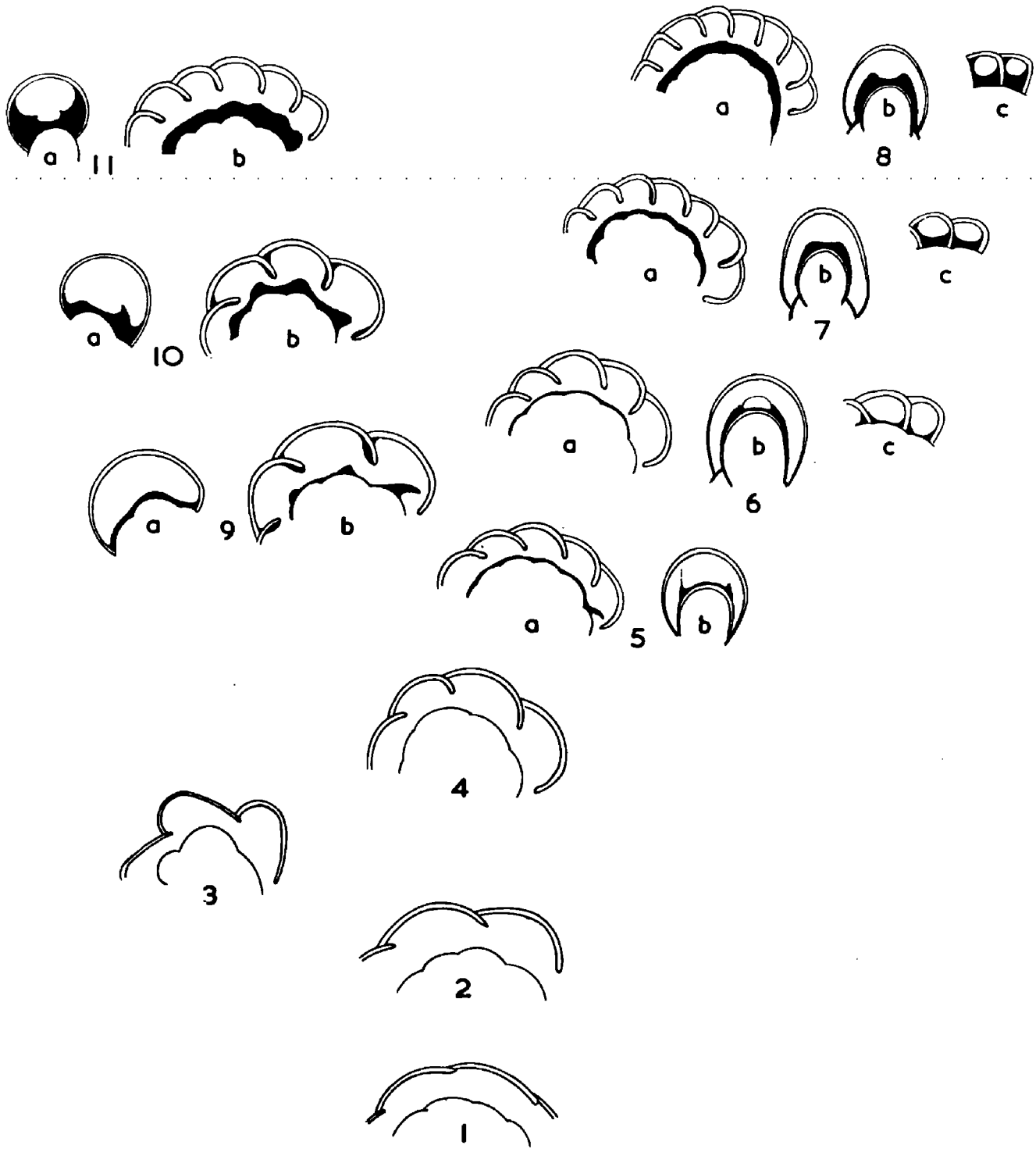
essentially identical to that of the protheca. There are however differences in the opacity of the two layers. It has been observed that the protheca in axial sections appears distinctly darker than the epitheca, while in saggital sections this differentiation is much less marked. This suggests some orientation of the rodlike granules, probably within the protheca. There is also a strong impression that the grains of the epitheca are rather coarser than those of the protheca, although this cannot be confirmed satisfactorily for reasons which have been discussed above. (p.6).

In more advanced fusulinids the protheca becomes lighter than the epitheca, and again this has been attributed to varying organic content by Skinner & Wilde (1954) and others. Indeed, Skinner & Wilde have gone so far as to suggest that there is a differentiation of organic material in the epitheca on the floor and the roof of the same chamber in such a way that the protheca appears more translucent only because it is sandwiched between the tectum and the very dark inner tectoria. They claimed that since the pores penetrated both protheca and epitheca they could not be responsible for the varying opacity of the wall. On the contrary, observation of their plates (Skinner & Wilde 1954, Plates 48-50) shows that the pores do not pass through all layers in a uniform

TEXT - FIGURE 3.

The development of chamber form and secondary deposits in endothyrid and primitive fusulinid foraminifers.

1. simple constricted tube producing pseudo-chambering typical of primitive tournayellids.
2. inflation of the tube with stronger constrictions forming primitive anteriorly directed short septa.
3. strong anterior inflation results in chernyshinellid type of chambering without true septa.
4. elongate sub-tubular chambers with strongly anteriorly directed chambers: width much greater than height.
5. elongate chamber form typical of Zellerella
   a.) thin basal layer of epitheca culminat-:ing in prominent curved hook in last chamber.
   b.) epitheca confined to thickening of septal ends in lateral part of chamber.
6. chamber form developed in primitive species of Paramillerella, with greater differenti-:ation of septa from the spiral wall and a


a
11
b
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b
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8
10
a
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a
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c
7
9
a
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a
b
c
6
a
5
b
4
3
2
1

TEXT - FIGURE 3. - cont.

more quadrate sagittal shape (the ratio of width to height decreasing).

a.) sagittal section;

b.) axial section;

c.) parallel sagittal section showing the development of pseudochomata.

7. the development of quadrate chambers with quite strong differentiation of the septa from the spiral wall. a.b.c. show the development of platform-like chomata, clearly modifying the peripheral contour in the interseptal part of the chamber.

8. the development of typical fusulinid chamber forms with rectangular chambers and septa strongly differentiated from the spiral wall. a.b.c. show the development of levee-like chomata forming a definite channel on the periphery between the septa.

9–11. show that the same basic modification of chamber form occurs in Endothyra, and illustrates the complimentary thickening of the epitheca which occurs in species of Endothyra from Lower to Middle Carboniferous.

a.) vertical axial section.

b.) horizontal axial section.

fashion, but reach their greatest concentration in the protheca. In general, the distribution of the pores accounts satisfactorily for the major changes in fusuline wall structure, while the physiological reason for variations in organic content are obscure, Furthermore, as has been discussed above, there are grounds for dismissing the concept of organic matter as an intimate constituent of the granular calcareous wall.

Chambers.

In general, the biocharacters of chamber form and chamber arrangement are mutually dependant. Thus basic changes in the plan of growth of the test are accompanied by major changes in chamber form, i.e. in the assumption of the rectilinear from the planispiral mode of growth. However, in so far as the endothyrids are consistent in their enrolled mode of growth, the biocharacter of chamber form is of greatest importance, as it is influenced by the trend towards increased subdivision of the test into chambers, during which the expression of chamber form is subordinated to the overall architecture of the test. This trend can be recognised in both the planispiral and plectogyral tests. (Text fig.3). Nevertheless, it must not be overlooked that in the change from plectogyral to

planispiral coiling certain modifications of chamber form do occur. Fundamentally this is the acquisition of a symmetrical arrangement about the periphery of the test with equal prolongations of the axial ends of the chamber towards the umbilicus. In contrast, in plectogyral tests the chambers vary continuously in form; their shape being governed by the position of the last whorl and the periphery of the penultimate whorl. (Text fig.3, Nos.4 & 5). The chambers always have an asymmetrical form with a constantly varying involute-evolute relationship to the earlier whorls of the test.

The subordination of chamber form to test architecture is expressed in a progressive change in the shape and overall dimensions of the chambers during the phylogeny of the group. The most primitive endothyrids, in sagittal sections, have chambers wider than they are high and with the septa anteriorly directed, forming a smooth curve with the outer wall. Such chambers are primitive and indicate their phylo-:genetic link with more primitive tubular septation as is seen in the Tournayellidae. (Text fig.3, No.6.). In the more advanced forms chambers tend to decrease in depth and become globular while the septa become more clearly differentiatied from the outer wall of the chamber. Eventually the chambers become higher

than they are wide, and the septa meet the outer wall in a right angle, with peripheral lobulation reaching a minimun. (Text fig.3).

Septa.

Septal characters cannot be considered independant of chamber form in the endothyrids for in most primitive genera there is no differentiation of the septa from the spiral wall. The progressive differentiation of the septa from the outer spiral wall of the chambers represents an important trend in endothyrid phylogeny, but it is fundamentally a function of the subordination of the chamber form to overall test shape. In their most primitive condition, as observed in the Tournayellidae, septa do not form the anterior face of the chamber, but simply the position of constriction of the subtubular chamber at its apertural orifice. With reduction of apertural diameter and inflation of the posterior portion of the tube, primitive chambering and septation arises in which the septa is still effectively a continuation of the spiral wall. As the subtubular chambers shorten they tend to become rather more inflated peripherally with a stronger anterior curvature, and it is chambering of this type which is present in primitive species of Endothyra and Zellerella gen.nov. Indeed, the septation in the

earliest chambers of some of these species shows a very close comparison to the outer chambers of Tournayella. The greatest septal complexity is attained in the subfamily, Bradyininae with the development of preseptal and postseptal lamellae, but this is associated largely with the development of subsidiary sutural apertural pores, and the major trend in endothyrid foraminifers is from septa, initially short, curved, and anteriorly directed, to long and straight lying approximately normal to the spiral wall (Text fig.3).

Aperture.

The greatest complexity of apertural form occurs in the Bradyininae with the development of cribrate aperture on terminal face together with subsidiary sutural pores. The characteristic apertural condition of the endothyrids is conservative, and is a basal lunate to semicircular opening at the base of the apertural face. Infrequent changes of growth plan from a spiral to a rectilinear condition necessitate changes of chamber form which result in simple terminal areal aperture (Endothyranella) and cribrate aperture (Mikhailovella).

It is established that the aperture is absent in a number of the more advanced and fusiform fusulinid

genera, and it has been assumed, largely without evidence, that a number of primitive forms, such as Millerella and Paramillerella, similarly do not develop an aperture. More careful study has shown that most of the short axised forms do develop an aperture, even although there is some evidence of its reduction to a somewhat vestigial condition in some species (Moore, 1964 p.296 and Anisgard & Campau, 1963 p.99). Although the apertural condition of a number of fusulinid genera requires further study, the evidence available at present suggests that the aperture finally becomes degenerate in association with increasing axial length, and possibly in response to increasing pore size.

POPULATION ANALYSIS.

The results of population analysis are discussed here only in so far as they are relevant to the systematic study. The main stratigraphical implications of the population studies will be discussed during the stratigraphical summary, while the actual technique whereby sufficient orientated sections were obtained for statistical study has been discussed in an earlier chapter.

As Burma (1948 p.758) has observed the fusulinids, as a group, have been treated in a quantitative manner more consistently than any other group of fossils.

This varies from typical tabulation of dimensions of the major biocharacters in a small number of specimens, to less frequent but more detailed graphical studies such as those of Lloyd (1964), or Chen (1934), and to comparatively rare and more complex statistical treatments (Burma, 1948 & 1950 and Morikawa, 1962). Despite this tradition, however, variation in fusulinid populations has been handled, with a few exceptions, in a subjective manner, and in most studies little attempt has been made to compare species except in a subjective and largely qualitative fashion. Primitive fusulinids, in general, lend themselves to statistical study for, while populations are often highly variable, their morphology can be expressed in terms of relatively few, and easily enumerated biocharacters but, until now, the major problem in attempting a statistical treatment was in obtaining the necessary number of orientated sections. For this reason only the data on a very small number of specimens is supplied in most systematic studies, and all too often the dimensions refer to sections in poor or unsatisfactory axial or sagittal orientations.

The data commonly reported in fusulinid studies are as follows - half length (axial) or total length, radius vector or total diameter, form ratio, tunnel angle, wall thickness, height of volution, septal or

chamber count per volution, and diameter of proloculum. Each parameter is normally reported in relation to the whorl number which reflects the rate of expansion of the spiral, and because of its logarithmic nature provides a useful 'time' character (Burma, 1948). On the other hand, Carter (1953 p.243) suggests that a more accurate comparison is obtained if the reference points for measurements and counts are taken at precise distances round the spiral thereby yielding data for the same degree of spiral growth in all specimens. However, neither means of comparison is strictly accurate for they both assume that growth is continuous. A major problem in the study of many fossil groups is the identification of equivalent growth stages, and this is clearly most acute in forms which display continuous growth and at the same time preserve no evidence of their ontogeny. Fortunately this problem does not arise in foraminifers, the majority of which show periodic growth and preserve their early stages within the test. Therefore, the proloculum represents the climax of the first stage of growth, and each additional chamber represents a precise growth stage at which the characters of the test may be compared. In tests coiled in logarithmic spiral the most accurate characterisation of the form would result from the comparison of the parameters of spiral length, axial

length, and radius vector at points predetermined by the number of chambers. Unfortunately, it would be impossible to recognise reference points defined in this way in axial sections, nor could their position be conveniently estimated. Furthermore, there is no convenient means of measuring the spiral length of a specimen under the microscope. In any single population the whorl number closely approximates to a growth stage for, in most species, the number of chambers in any given whorl is similar. In comparison with a different species the whorls may contain a greater or smaller number of chambers, and thus, is not in the strict sense an equivalent growth stage but, in so far as each whorl is the direct function of spiral length, it is a convenient unit against which comparison can be, and traditionally has been, made.

In this study the accuracy with which measurements could be made was limited through studying the specimens in reflected light, which does not allow observation at magnifications much greater than 200 diameters. Consequently it was not possible to measure the thickness of the protheca with sufficient accuracy to provide meaningful results. This is not, however, a serious disadvantage for the thickness of the protheca is not a biocharacter of great significance in Endothyridae. Moreover, in the majority of studies the dimensions

of the protheca are combined with the basal layer of epitheca in the spirothecal thickness thereby obscuring the significance of both biocharacters. The external diameter of the proloculum is most typically recorded, but here the internal diameter is utilised for it has the advantage that it eliminates the ambiguities of differentiating the prolocular wall from the epithecal coating and the wall of the embracing chambers.

The tunnel angle is disregarded in this study for, as has been pointed out by Burma (1948 p.759), it is a compound measure, being a function of the width of the tunnel and the radius vector. Furthermore, the majority of species of Paramillerella lack chomata, and it is possible to measure the tunnel angle only where the plane of section meets a septum. The value of this measure is further reduced by the fact that the tunnel is commonly asymmetrically arranged in relation to the sagittal plane of the specimen.

Although in many studies they have been ignored or approximated, the septal or chamber counts are here regarded as of fundamental importance, and are recorded at successive half whorls with the diameter of the test. The advantage of recording diameter at each half whorl is that radius vector, or the height of the whorl (volution) can be derived for comparison with other studies where these characters have been utilised and,

furthermore, it provides a more detailed and complete characterisation of the test.

On axial sections the diameter was again measured at each half whorl along with the axial length, (maximum width of whorl) and from these dimensions the ratio of length to diameter, or form ratio, can be calculated. The diameter measured on axial sections is not comparable with sagittal sections because, as has been demonstrated by Burma, the position of the whorl can only be estimated within half a whorl. In most of the populations observed the diameter measured in axial sections gives a value less than that in sagittal sections (Table 3), while V, the coefficient of variability, is generally a little higher. Although comparison of the dimensions of axial sections is used almost exclusively in systematic studies of Russian authors, in fact, this provides the least accurate comparison and should be used only in determining form ratio.

TABLE 3.

Limestone	Locality	1st Whorl Sagittal Diameter (microns)	2nd Whorl Axial Diameter (microns)
1. Lyoncross	Whitecraigs	76	75
2. Lyoncross	Clarkston	77	73
3. Lyoncross	Craigburn	94	89
4. Lyoncross	Muirkirk	94	88
5. Orchard	Strutherhill	72	74
6. Orchard	Poniel Water	73	70

(1,2.*Paramillerella indicis*, sp.nov.: 3,4.*P.ayrensis* sp.nov.: 5,6.*P.radiata* (Brady).

In Table 3, the sagittal diameter measured on populations from different localities of the same horizon are more accurate than the axial diameter at the same locality. Moreover, at different localities the difference in axial diameter approaches statistical significance in some instances.

The majority of the measurements, as has been discussed, were made on sections observed on polished slices of limestone. The advantage of this method of study is that, providing the population has not previously been selectively modified by sedimentological or diagenetic factors, sampling is effectively random; the sample of the population being selected by the cut of the saw, unlike material obtained from shales

where sieve size and the bias of hand picking the sample can introduce sampling errors. Preferred orientation of the specimens in the limestone may introduce some bias in the number of axial or sagittal sections observed in a slice, but this can generally be overcome by slicing the rock parallel to and at right angles to bedding. From the point of view of obtaining a sample of maximum contemporaneity it is best to utilise sections parallel to a single bedding plane but this is commonly impracticable and, for the most part, material from a single hand specimen 20-40 cubic inches, gives satisfactory results, yielding samples of up to 50 specimens in both axial and sagittal planes of section.

For each of the measured biocharacters the following basic statistics have been calculated and are stated for each half whorl.

N = the number of specimens in the sample containing the appropriate number of whorls.

x = the mean for the character at each whorl.

s = the standard deviation.

ex = the standard error of the mean.

V = coefficient of variation.

OR = the observed range of the character at each half whorl.

In addition, from the mean diameter of each whorl, a spiral ratio is computed which compares the diameter at successive whorls and provides an indication of the rate of expansion of the whorl. This measure was suggested by Davies (1934) for the study of the spiral of nummulitids and allied genera, and as he pointed out, provides a more precise measure of the type of coil than terms such as tightly or loosely coiled. It is a somewhat cruder measure than the spiral angle but is more readily obtained. Finally the whorl frequency is recorded as an indication of the predominant growth stage in the population.

Over 1,040 specimens of Paramillerella have been examined involving twelve populations ranging in sample size from 42 to 140 specimens. In every group studied so far, differences in samples drawn from the same horizon, but differing localities, are insignificant, and are less than differences observed between populations from differing stratigraphic positions. The relationship is, of course, conveniently emphasised by the rhythmic character of sedimentation which produces, for the most part, thin and distinct limestone units.

The dimensions of the populations are highly variable and the range of the coefficient of variability lies well outwith typical values for a homogeneous sample as discussed by Simpson (1941) and Simpson &

Roe (1963). The range suggested by Simpson, from 4-10 is based mainly on experience in mammals, and may not be directly applicable in study of protozoans. Very little accurate data are available on this parameter in invertebrate studies and it is not absolutely clear how the values obtained should be interpreted. The figures are, however, reasonably consistent for each character, which suggests that whatever feature contributes to the high value of the coefficient of variability, it is inherent in all of the populations. The most obvious sources of error; inclusion of a range of growth stages or more than one species in the sample, do not appear to be applicable. Most striking is the high value of V obtained for the diameter of the proloculum. The maximum range observed in the populations was from 14-27, with typical values from 17-22. Inaccuracies of measurement discussed above, together with lack of control in obtaining the maximum proloculum diameter in sections, undoubtedly contribute to this high figure, but errors of comparable magnitude are likely in the measurement of the first whorl, and therefore, this cannot be the major source of the high variability. The most obvious explanation for the large V is that, while the proloculum in itself undoubtedly represents a growth stage, it will, nevertheless, provide an

inhomogeneous sample unless the individual reproductive stage can be identified. Thus the high value of the coefficient of variability for proloculum diameter may be regarded as evidence of dimorphism in Paramillerella. The high values of V for prolocular diameter are not maintained in the diameter of the whorls, although V is still high, ranging from 10-18, with mean values of 12-15. In contrast the chamber counts, though variable, do not show particularly high values of V, and these normally fall within the range 5-11, with mean values of 7-9. The implication is, therefore, that the dimorphism, or high variability of the proloculum, has a greater influence on the diameter than on the number of chambers in a given whorl. It has been suggested both by Le Calvez (1938) and Carter (1953) that the volume of a chamber is proportional to the volume of protoplasm occupying pre-existing chambers and, therefore, while diameter fluctuates markedly, the number of chambers remains relatively constant. Thus in a population from the Lyoncross Limestone at Overlee, Clarkston, an individual with a proloculum diameter of 40 microns may have 6 chambers in the first whorl with a diameter of 90 microns, and 9 in the second whorl with a diameter of 178 microns, while another individual in the same population, with the same chamber counts, and a

proloculum diameter of 20 microns, may have a diameter of 68 microns in the first whorl, and 110 microns in the second. This relationship can be confirmed statistically by splitting the population into two groups according to the diameter of the proloculum which ranged from 17-43 microns, with a mean of 24 microns. A diameter of 25 microns was taken as the dividing line and comparative figures for the three groups can be seen in Table 4.

TABLE 4.

		2nd Whorl Chambers	2nd Whorl Diameter (microns)	3rd Whorl Chambers	3rd Whorl Diameter (microns)
Whole Sample 17-43		9.1	145	11.73	262
Prolocula	25	9.0	138	11.94	246
Prolocula	25	9.2	160	11.84	281

The means of Table 4 may be compared by the formula,

$$t = \frac{6d}{d}$$

where $6d = \sqrt{\frac{S_1^2}{N_2} + \frac{S_2^2}{N_1}}$ and $d = x_1 - x_2$

S = standard deviation, N = number of specimens, x = the mean.

Considering first the chambers in the second whorl,

$$6d = \frac{0.162}{31} + \frac{0.35}{37} = \pm 0.12 \quad d = 0.2$$

therefore, $t = \frac{0.2}{0.12} = 0.1$, and hence, P = 0.955

similarly in the third whorl,

$$d = \frac{0.796}{29} + \frac{0.939}{35} = 0.23 \quad d = 0.46$$

therefore, $t = \frac{0.46}{0.23} = 2$, and hence, P = 0.955

In neither case is their a significant difference between the means of the two groups, while, in contrast, the differences in diameter yield a statistically significant result.

At the second whorl, $d = \frac{54}{31} + \frac{49}{37} = 5.2$, $d = 22$

therefore, $t = \frac{22}{5.2} = 4.2$, and hence, P 0.997

At the third whorl, $d = \frac{114}{29} + \frac{178}{35} = 8.77$, $d = 35$

therefore, $t = \frac{35}{8.8} = 3.96$, and hence, P 0.997

Thus the correlation of the size of the proloculum with the diameter of successive whorls is demonstrated, while, because of their consistent volumetric ratios, the number of chambers remains relatively constant. The conclusion is, therefore, that for any given diameter, or spiral length, a test with a small proloculum will contain more chambers than one with a large proloculum: a relationship which has already

been established by Carter (1953) in Operculina. Furthermore, it demonstrates, as Burma (1948) points out, that an unthinking attempt to split a group of individuals will probably be successful, and more probably wrong. Thus Cooper (1947) has based three species, Millerella zelleri, M. chesterensis, and M. kinkaidensis, on a single group of specimens from a one foot shale horizon, differentiating them on proloculum size and character of the juvenarium: characters which, as has been discussed, control the absolute dimensions of the whorls, and allow the recognition of artificial size groups.

How far absolute size may be taken as a specific character, thus becomes a factor of crucial systematic importance, particularly in view of the fact that ecological factors are reported to have a direct influence on size. The evidence is, unfortunately, somewhat contradictory, and vague regarding what is meant by such terms as 'dwarf', or larger size. It is particularly important to recognise whether change in size results from larger or small chambers or simply from a decrease or increase in the number of chambers present in the test. Unfavourable conditions of oxygenation and salinity (Miller, 1953, Le Calvez & Le Calvez, 1951 and Lalicker, 1948), and nutrition (Boltovskoy, 1956) have been suggested as the cause

of dwarf and depauperate faunas. In contrast, in unfavourable conditions of temperature, or temperature and salinity, where frequency of reproduction and rate of growth decline, it has been suggested by Bradshaw (1957) that larger specimens may be expected. In the latter case, increase in size is attained by the addition of chambers over a longer period of time, assuming normal nutritional conditions. The resulting specimens would differ from those occuring in optimum conditions only in having additional chambers and whorls, and not in having larger chambers and larger whorls, as has been implied by Loeblich & Tappan (1964) in regarding Endothyra of the Salem and St. Louis limestones as giant forms resulting from unfavourable environmental conditions.

Although it is believed that protoplasmic volume is the ultimate mechanism controlling chamber addition, it should be noted that Lister (1895) and Jepps (1942) reported regular additions of chambers, one every other day over a period of three months, in young individuals of Elphidium crispum. If chamber addition was simply a periodic or rythmic function of growth then chamber size, within the limits of the architecture of the test, would reflect the relative nutritional success or failure of the individual, and individuals in a consistently poor nutritional environment may add a smaller chamber

than those enjoying optimum conditions. In so far as marine environments are comparatively uniform in any one geographic location, the conditions enjoyed by a single individual in relation to its fellows are not likely to remain uniformly good or bad. For the majority of the population an average condition will be experienced, leading to consistent dimensions for the population. In a different environment the species may enjoy quite different nutritional conditions and, therefore, the average dimensions of each chamber, and thus of the whole test, may differ. If this relationship was wholly accepted, then facies would play an overwhelming role in the systematic study of fossil foraminifers, and absolute size would have very limited significance.

An interesting comparison is available in populations of P. (Paramillerella) obtained from the Lyoncross limestone (Text fig.19). From two localities in the Central Coalfield area of the Midland Valley of Scotland a small form was obtained of which the dimensions are given in Tables 13,14 and 15,16. From two localities in the Ayrshire and south Lanarkshire Coalfields another form was obtained, having an identical chamber count (Text fig.24 and Tables 25,26 and 27,28) but differing in absolute size. Although all four localities are considered to be at the same

stratigraphic level, located by borehole control, and are believed to be contemporaneous, so far as can be determined, it is probable that they were originated in separate basins partially or wholly isolated from each other by land or submarine ridges. Thus the populations from the two basins could be regarded as belonging to the same species displaying large size in marginal conditions of temperature and salinity, or through experiencing very much richer nutritional conditions in one basin than the other. Such an explanation does not appear to be acceptable, however, if the volume of protoplasm is a controlling factor in growth. It has been reported by Jepps (1942) that in Elphidium an unfavourable nutritional environment leads to degeneration involving the slowing of the activity of the pseudopodia with the gradual loss of their granules which is associated with a definite thinning and decrease in volume of the cytoplasm. Elphidium was observed to be able to withstand long periods of starvation, artificially in the laboratory and during the winter months in the sea, and was seen to return to normal growth after a week to ten days of good living. These observations certainly suggest that protoplasmic volume controls the growth of the test but is not clear how far nutrition and other environmental factors may be able to modify this

fundamental physiological control. Le Calvez (1938) has suggested that seasonal changes in temperature, salinity, and density have relatively little effect on chamber form, although he considered the surface tension of the cytoplasm and its surrounding medium to be of importance.

Although the evidence is not entirely conclusive, it suggests that in logarithmically coiled forms, such as Paramillerella, the absolute size at any given whorl or spiral length will be determined, first by the reproductive cycle and the range of sizes of proloculum which results, and secondly by the size of chambers formed, which appears to be controlled by the genetic factors of the individual species (Le Calvez, 1938). Therefore, to establish true size differences it is necessary to compare the volumetric relationship of the chambers, and establish the normal range of proloculum diameter. This is best accomplished by population studies in which the variability can be assessed and the ranges and means of the biocharacters established. Returning to the example of the populations observed in the Lyoncross limestone, comparison of the dimensions shows that although the populations differed in size, the ratios of the characters are, in fact, very similar: form ratio, spiral ratio, and ratio of proloculum diameter to later whorls. In general

proportions of the tests of the two populations are similar, however, the range and mean diameter of the proloculum differs, and the ratio of chambers to diameter, the Ayrshire populations having 27 chambers at a diameter of 320 microns, while the populations from the Central Coalfield have 33 chambers. Thus, although they undoubtedly show a great similarity of form, particularly in axial sections, these populations are regarded as representing two distinct species. It is worth noting, however, that these populations show a distinct overlap in the range of their biocharacters, and their differentiation could be a difficult matter if reliance is placed on a small number of axial sections, as is customary in many systematic studies. In populations from the Upper Limestone Group, the comparison of mean number of chambers against the mean diameter at successive whorls (Text figs.23 & 24) shows that this is a ratio of great stratigraphical and systematic importance.

The results of this study suggest that samples of 25 specimens adequately characterise a population, although with a sample of this size, it is often found that the number of specimens developing a full complement of whorls drops to a point where they no longer provide adequate data for the final whorls. The final whorl commonly shows the greatest variability for it is not

uncommon to find that the last few chambers of a complete adult specimen become very much more inflated than those of the preceding whorls and, thus, the last whorl has not many more chambers than the penultimate whorl. Since measurement is made from the proloculum outwards, in some cases the inflated chambers of the final half whorl are not considered, and, in many specimens, the last half whorl with its more strongly inflated chambers is broken, crushed and distorted. Thus measurements of the final whorl are most variable, and provide the least reliable comparison of paramillerellid tests. Samples of less than 20 specimens, while undoubtedly of value, do not yield entirely reliable and consistent results because of the high variability of the populations.

As quantitative methods have been progressively applied in palæontology, the inadequacies of traditional typological methods have become increasingly apparent. Realisation has become more widespread that what the systematist should describe are populations and not individuals or types. Unfortunately, the step from realisation to application is not a simple one, and contradictory views are expressed regarding the solution of this problem. The extremes of viewpoint may be summarised, on the one hand, by Arkell (1956, pp.97-99) who considers the species in palæontology as an

artificial unit determined subjectively against the experience and character weighting selected by the 'competent' systematist. Attempts to rationalise the conception of a species in palæontology he dismissed as semantical. On the other hand, while arguing for quite different reasons that the species is artificial, 'a mental construct without objective existence', Burma (1949 p.369) sees the solution to the problem in species defined on an arbitrarily selected unit of their parameters. Between such extremes lie compromises suggested by such workers as Davies & Trueman (1927 pp.218-219), Trueman & Weir (1946 pp.XX-XX1), Eagar (1952 pp.1-4, 1956 pp.111-116), or the slightly more statistical approach to morphotypes adopted by Sylvester-Bradley (1958).

In systematics of Upper Palæozoic smaller Foraminifera conventional palæontological descriptive methods have been applied, and, indeed, it could fairly be said that in work of Russian authors the type concept has been carried almost to its ultimate extreme. This arises through the study of foraminifers in random sections, and without thorough morphological analysis of species or genus, morphospecies are commonly identified on the basis of a single random fragment whose characters are determined more by the attitude of the section to the original specimen, than any intrinsic morphological

attribute of that specimen. The crudity of this method, despite expectation, does not overwhelm the fundamental reality of evolutionary change, although the details become seriously blurred. As a stratigraphic tool, it is a blunt instrument, yet by its qualitative assessment of variants, through comparison in the conventional manner of morphotypic species in charts of range and abundance, provides a workable zonation. Cummings (1958, 1961) has argued that, in dealing with random fragments in thin section, 'identification of the conditions of the biocharacters should largely replace that of the individual specimen', which may indicate the presence of a particular family or genus but rarely that of a morphospecies. Thus fossil assemblages may be regarded as a summation of the conditions of various biocharacters of differing families and genera rather than a community of species. Such a technique simply hedges the nomenclatorial problem in order to facilitate its stratigraphic application, and apart from its simplicity of application, its end product is a zonal scheme no more detailed than that obtained in the conventional manner discussed above.

In an attempt to obtain more detailed stratigraphic subdivision of the Upper Limestone Group (F.Z.10, Cummings, 1961) greater emphasis has been placed on

the examination and estimation of the characters of the populations. Thus, while Cooper (1947), St. Jean (1958), and Kanmera (1952), have identified a number of morphospecies from a single community at a single horizon and locality, here, by definition, (Mayr, 1949, Burma, 1948), such populations are regarded as a single species. Limitations on this hypothesis must of course be recognised (George, 1956 p.127), but, as Burma has suggested, it should be the starting point of systematic study. In other words the population should be considered innocent until proved guilty. In the present study, examination of population characters, rather than those of individuals, provides a far more revealing and detailed stratigraphic subdivision than could have been attempted by conventional methods. With this justification all species of Paramillerella are described with reference to populations rather than to types, although the name of the species is applied to an individual displaying, so far as possible, the modal characters of the population. Thus, the systematist of conflicting viewpoint may choose to accord more peripheral variants of the population separate status, but this would simply blur the fact that population structure is a very exact measure of evolutionary stage, hence geological age. Only populations, not individuals evolve (Newell, 1956 p.79).

For the most part, the difficulties of subdivision of the lineage or chronocline recognisable within the paramillerellids of the Upper Limestone Group are solved by the arbitrary subdivision of cyclical sedimentation, and differences in characters lie well outwith the arbitrary statistical units suggested by Burma (1948 p.740) or Sylvester-Bradley (1951), but would lie well within those of Mayr, Linsley & Usinger, (1953 p.142) or Haldane, (1949 p.42). Application of the subdivisions advocated by the latter authors would lead to groups far broader than those typically recognised in present systematic treatment of paramillerellids. While this may be in part a reflection of the inadequacies of the method, if one is, in fact, dealing with a chronocline then the sub-:divisions of Burma and Sylvester-Bradley are valid and useful in a stratigraphical context. Accordingly, in a single instance, subspecific rank has been extended to populations whose means lie just beyond the 95% limits of confidence.

SYSTEMATICS.

In recent years the phylogeny and systematics of endothyrid and primitive fusulinid foraminifers have been the subject of a number of major studies, notably Reitlinger (1950, 1958), Rauser-Chernoussova & Fursenko (1959), Rozovskaya (1961, 1963), and Loeblich & Tappan (1964). The full historical development of research on this important group of foraminifers has been fully reviewed in the above studies, and the present discussion is concerned mainly with present condition of classification.

Although Endothyra was recognised at an early date (Dunbar, 1933, 1940, Dunbar & Henbest, 1942) as an ancestor of the fusulinids, a complete classificatory dichotomy has, for the most part, been maintained between the two groups. The classification of Glaessner (1945) provided the sole exception and recognised the close phylogenetic and structural parallels of these families by including them in the superfamily Endothyridea. Wood (1949) also emphasised the fundamental similarity in wall structure between Endothyra and the fusulinids but, nevertheless, later classifications (Cushman, 1948, Pokorny, 1958, Rauser-Chernoussova & Fursenko, 1959 and Rozovskaya, 1963) continue to maintain a classificatory isolation

of the families although the studies of Thompson (1942), Scott, Zeller & Zeller (1947), Zeller (1950), Anisgard & Campau (1963), and Moore (1964) show that the families are much more closely related than current classificatory systems lead one to expect.

A review of the biocharacters of endothyrids and fusulinid foraminifers shows that, at least as present classifications stand, there is no unique and characteristic group of biocharacters which would distinguish one group to the exclusion of the other. The specialisations of wall structure observed in the fusulinids are foreshadowed in the development of alveolar structure in Bradyina, and the development of pores in Endothyra, and, as has been emphasised by Wood (1949 p.239), the fundamental basis of the wall in both families is fine grained homogeneously granular calcite.

Both families secrete secondary skeleton of finely granular calcareous calcite and are capable of modifying the interior of the test through resorption. The axial fillings of Mediocris foreshadow this characteristic type of epithecal modification in advanced fusulinid genera. There is however, an obvious contrast in the development of epitheca in Endothyra as vestibular hooks and ridges across the floor of the chamber, and reaching a maximum in the final chamber, and the

development of chomata parallel to the tunnel with a maximum in the earlier part of the test. Nevertheless, some authors, notable Anisgard & Campau (1963) and Rozovskaya (1963), would overlook this basic characteristic and consider species such as Endothyra spiroides, or Endothyra symmetrica Zeller as primitive fusulinids.

At one time it was believed that the so called primitive fusulinids Paramillerella and Millerella did not possess an aperture but this has proved to be an unwarranted assumption, and it is now clear that the majority of these forms have an aperture. The fact that the tunnel is enlarged by resorption of the original apertural orifice cannot be considered a significant feature as has been argued by Moore (1964), for it has been established by Zeller (1950) that this same process occurs in Endothyra. Clearly in the past insufficient attention has been given to the aperture in fusulinid foraminifers, and its classificatory role is uncertain. There are a number of genera, Eoschubertella, Pseudostaffella, Ozawainella, etc., in which the apertural characters remain to be established.

The mode of enrolment has also been considered as a classificatory key but, although the fusulinids are predominantly planispirally coiled it is not exclusively so, and such characteristic forms as Pseudostaffella and Eoschubertella show marked axial rotation throughout a

major portion of the test, while such typical endothyrids as Mediocris Loeblichia and Zellerella gen. nov. are planispiral. Furthermore, axial rotation of the initial portion of the test is so characteristic a feature of fusulinids that it lead to the prediction that Endothyra was the ancestral form of the fusulinids before any of the intermediate primitive forms had been recognised.

At first sight axial length would appear to be a biocharacter useful in separating fusulinid from endothyrid forms, particularly since recent evidence suggests that the loss of the aperture in fusulinids occurs in association with increase in axial length. However, for reasons which are as much historic as phylogenetic, a number of short axised forms have been considered as fusulinids. This would appear to stem from Moeller's (1878) identification of primitive forms as Fusulinella, followed later by Ozawa's (1925) grouping of all forms coiling on a short axis in genus Staffella. The stratigraphic contemporaneity of many of these forms with more complex and more typical fusulinids would appear to have contributed, as much as their structural develop-:ment, to their acceptance within that family. Brady (1876) regarded the planispiral short axised forms as species of the genus Endothyra, and in a sense,

following this lead, Cummings (1961) placed the primitive fusulinids with a short axis of coiling in the family Endothyridae.

Finally chamber form may be considered as a determining biocharacter for, while most typical fusulinids develop rectangular chambers with radial septa strongly differentiated from the spiral wall, the chambers of endothyrids are typically inflated with curved, anteriorly directed septa, poorly differentiated from the spiral wall. This character alone, however, does not serve to distinguish the two groups, for the development of one type of chamber form from the other can be observed during the phylogeny of Paramillerella. Moreover, the distinction becomes further eroded in more advanced species of Endothyra in which chambers begin to assume a more rectangular form.

The purpose of this review may appear negative in its suggestion that none of the biocharacters can be used satisfactorily in classification, but the main purpose is to emphasise the close morphological parallels and clear phylogenetic relationship between endothyrid and fusulinid foraminifers which is not reflected in current classifications. The only concession to this relationship in recent classification has been made by Loeblich & Tappan (1964) in grouping

superfamilies Endothyracea, and Fusulinacea in the suborder Fusulinina, but this was based on the possession of a granular calcareous wall structure, and led to the inclusion of groups within the super-:family Endothyracea and the suborder Fusulinina whose relationships to the family Endothyridae are very much more obscure than the relationship of that family to the Fusulinacea. Moreover, although Loeblich & Tappan have stressed the importance of wall structure they have overlooked its significance in families such as Haplophragmellinae, grouping together genera such as Cribrospira, Mikhailovella, and Mstinia, which most authors (Reitlinger, 1958, Ganelina, 1956 and Rozovskaya 1963) would consider of proven and differing phyletic origin. Similarly the subfamily Loeblichiinae is artificial and groups together an oddment of genera none of whose characters or phylogenies is very well understood. With the exception of Loeblichia itself the remaining genera would appear to be more logically placed outside the Endothyridae.

While the classifications of Reitlinger (1958), Rauser-Chernoussova & Fursenko (1959) and Rozovskaya (1963), are poor in that the obscure the relationship of fusulinid foraminifers and their endothyrid ancestors in separate order Endothyrida and Fusulinida, in detail, their treatment at generic level follows a more logical

course than that suggested by Loeblich & Tappan (1964). However, a major weakness in these classifications is the subfamily Endothyrinae of Reitlinger, or Quasiendothyridae of Rozovskaya (1961), with the genera Quasiendothyra, Paraendothyra, Dainella, Loeblichia, Planoendothyra, and Eostaffella; Rozovskaya having excluded the genera Janischewskina and Cribrospira from Reitlinger's family on the grounds of their obvious structural and phyletic relationship to Bradyina.

Study of this family shows that there are serious discrepancies in the projected phylogenies of its genera. Regarded as having been derived from Quasiendothyra by Reitlinger (1958), Planoendothyra is here regarded as a junior synonym of Endothyra, and, even were this synonymy rejected, it is clear that Planoendothyra, as represented by its type species Endothyra aljutovica Reitlinger, is the culmination of a well defined bioseries occurring in Endothyra in Namurian and Middle Carboniferous strata. Thus should this form be accorded generic status it must be within the Endothyridae.

The genera Loeblichia and Novella show a marked morphological similarity despite their assignation to separate families and orders, and they would appear to represent no more than the opposite ends of the same phyletic line. Great stress has been laid on

the altered nature of the wall in Loeblichia (Cummings, 1955, and Fomina, 1958) but this is believed to be exaggerated and, therefore, Loeblichia is regarded as a junior synonym of Novella. Neither of these forms, nor the closely related genus, Endostaffella, is considered to have evolved from quasiendothyrids, which form a highly specialised and advanced group of forms in Upper Devonian and Tournaisian strata. Quasiendothyrids are specialised in having a double wall, very heavy and unusually developed secondary deposits, highly irregular pattern of coiling, tendency to uncoil, and very commonly a cribrate aperture. None of these characters is passed on to the Visean forms which show quite simple structures, are strikingly lacking in secondary deposits, and resemble Quasiendothyra only superficially in the pattern of coiling. Such an abrupt simplification of structure in phylogeny is contrary to the normally observed pattern of development in most Upper Palæozoic foraminifers in which tests of simple structure undergo progressive elaboration. Reitlinger (1961 p.27) argued that the great variability and instability of most of the morphological characters of Quasiendothyra, together with the appearance of a large number of characters fixed only very slowly, during evolution, suggested a period of evolutinary plasticity, or morphological experiment in the order

Endothyrida, but, while the group is primitive in its highly irregular 'glomospiral' type of coiling, the protheca, epitheca, chamber form, and apertural character provide a unique combination of specialised, phylogenetically advanced biocharacters. Thus the quasiendothyrids are not regarded as having had a directly ancestral role in the phylogeny of the Endothyridae and, indeed, like a number of other Devonian foraminifers their relationships to later groups are not entirely clear.

An unusual feature of the genus Mediocris, type species Eostaffella mediocris Vissarionova, is the fact that it has not yet been figured in sagittal section, and its relationship to Plectogyrina, type species Plectogyrina fomichaensis (Lebedeva) in Rauser-Chernoussova & Fursenko (1959, pl.V. fig.12), not yet figured in axial sections, would appear to require further study. The broadly rounded periphery and evidence of a degree of axial rotation in the early whorls of this form suggest that it is more appropriately assigned to the subfamily Endothyrinae.

Following is an outline of the classification adopted herein with the superfamily Endothyracea as proposed by Glaessner (1945) within the suborder Fusulinina as proposed by Loeblich & Tappan (1964).

Suborder FUSULININA Wedekind, 1937.

Superfamily ENDOTHYRACEA Brady, 1884.

Family ENDOTHYRIDAE Brady, 1884.

Subfamily Endothyrinae Brady, 1884, with the genera;

Endothyra Brown, 1843, sensu Brady, 1876.

Endostaffella Rozovskaya, 1961.

Endothyranella Galloway & Harlton, 1930.

Globoendothyra Reitlinger, 1959.

Mediocris Rozovskaya, 1961.

Mikhailovella Ganelina, 1956.

Novella Grozdilova & Lebedeva, 1950.

Zellerella gen. nov.

Subfamily Bradyininae Reitlinger, 1950, with genera;

Bradyina Moeller, 1878.

Glyphostomella Cushman & Waters, 1928

(= Pseudobradyina Reitlinger, 1950)

Cribrospira Moeller, 1878.

Endothyranopsis Cummings, 1955.

Jansischewskina Mikhailov, 1935

(= Samarina Rauser-Chernoussova and Reitlinger, 1940).

Khalerina Kochansky-Devide & Ramovs, 1955.

Subfamily Ozawainellinae Thompson & Foster, 1937

Ozawainella Thompson, 1935.

Millerella Thompson, 1942.

Paramillerella Thompson, 1951

Reichelina Erk, 1941.

Pseudostaffella Thompson, 1942.

The genera, Leella Dunbar & Skinner, 1937, Rauserella Dunbar, 1944, and Toriyamaia are transferred to the subfamily Schubertellinae.

Family STAFFELLINDAE Miklukho-Maklay, 1949.

Pseudoendothyra Mikhailov, 1939.

Nankinella Lee, 1933.

Staffella Ozawa, 1925.

Sphaerulina Lees, 1933

Pisolina Lee, 1933.

Family QUASIENDOTHYRIDAE Rozovskaya, 1961.

Quasiendothyra Rauser-Chernoussova, 1948.

Klubovella Lebedeva, 1956.

Dainella Brazhnikova, 1962.

Paraendothyra Chernysheva, 1940.

Family FUSULINIDAE von Moeller, 1878.

Subfamily Schubertellinae Skinner, 1931.

Subfamily Fusulininae von Moeller, 1878.

Subfamily Schwagerininae Dunbar & Henbest, 1930.

Family VERBEEKINIDAE Staff & Wedekind, 1910.

Subfamily Verbeekininae Staff & Wedekind, 1910.

Subfamily Neoschwagerininae Dunbar & Condra, 1928.

Suborder FUSULININA Wedekind, 1937.

Superfamily ENDOTHYRACEA Brady, 1884.

Test fully septate, multichambered, enrolled planispiral, or plectogyral, discoidal, spherical, fusiform or sub-cylindrical in shape, sometimes with a rectilinear stage; chambers not labyrinthine but in advanced forms subdivided into regular chamberlets; protheca calcareous, constructed of finely granular homogeneous finely granular calcite, exceptionally with certain amount of incorporated calcareous fragments, commonly with pores ('fibrous'), or simple to complex alveolar structure; interior of test modified by resorption, and by deposition of epitheca as thin basal coatings, sutural deposits, vestibular hooks and ridges, axial deposits, pseudochomata, chomata, and parachomata; aperture in simple forms, terminal, basal, lunate, occasionally cribrate, areal, or complex, absent in advanced forms; tunnel, tunnels, or foramina typically produced through resorption of septa in advanced forms, through enlargement of the apertural orifice in primitive forms.

Discussion:

This is essentially the conception of the superfamily proposed by Glaessner (1945 p.107) and, although several

authors, including Glaessner, (1963 p.11) Cummings (1955A, B), and Loeblich & Tappan (1963), argue that the similarities of wall structure in Nodosinellidae, Tetrataxidae, Biseriamminidae, Archaediscidae, Lasiodiscidae, Palaeotextulariidae, Ptychocladiidae, etc., warrant their inclusion within the superfamily Endothyracea, it is considered that in none of these families, with the possible exception of the Palaeotextulariidae which Cummings (1955B) regarded as having evolved from a coiled endothyrid ancestor, is there a clearly established phylogenetic link with the endothyrids. Furthermore, in many instances, comparison of wall textures are superficial. The fibrous element in the wall of the Tetrataxidae and Lasiodicidae, Palaeotextulariidae, and Archaediscidae is probably not an analogous structure in origin or function. In the classification adopted by Rauser-Chernoussova & Fursenko (1959) the Archaediscidae and Lasiodiscidae were considered to be Familiae Incertae Sedis, while the Tetrataxidae and Palaeotextulariidae were assigned to the orders Ataxophragmida and Textualriida respectively. In contrast, as Glaessner (1945 p.87 and 1963 p.10) has emphasised there is little doubt that the Fusulinidae are derived directly from the Endothyridae; a phylogenetic interpretation few authors would seriously contest. Thus the idea

expressed by Glaessner (1963 p.10) and inherent in the classifications of Loeblich & Tappan (1964) and Rauser-Chernoussova & Fursenko (1959), that it is more convenient to consider the Fusulinidae as a separate superfamily, seems a wholly subjective and artificial systematic artifice.

The Tournayellidae are considered to be very closely related to the Endothyridae, and if they are not the direct ancestors, they represent a parallel offshoot from the ancestral stock from which the majority of Carboniferous endothyrids were derived. The tournayellids are not, however, included within the Endothyracea because of the primitive subtubular, non-septate to pseudoseptate condition of their tests, which demonstrate unambiguously their primitive character and their affinities to an 'ammodiscid' ancestor.

Family ENDOTHYRIDAE Brady, 1884.

Test chambered, enrolled, complanate, discoidal, or globose, planispiral, or plectogyral, sometimes uncoiled; septa plane; aperture simple, terminal, basal, lunate, or less frequently, cribrate areal, or complex.

Subfamily ENDOTHYRINAE Brady, 1884.

Test complanate, discoidal to nautiloid, plectogyral, approaching or becoming planispiral in adult whorls, involute or evolute to uncoiling; number of whorls typically less than 5; chambers inflated, elongate to quadrate in sagittal sections, usually few in a whorl; peripheral margin broadly rounded; septa plane, convex, anteriorly directed, poorly differentiated or undifferentiated from spiral wall; protheca finely granular, homogenous, or with pores ('fibrous'); epitheca forming basal connecting deposits, and typically forming vestibular hooks and ridges, more rarely pseudochomata, or axial deposits; aperture simple terminal lunate, areal or cribrate.

Genus ENDOTHYRA Brown, sensu Brady, 1876.

Endothyra. Phillips in Brown, 1843 (nom. conserv. I.C.Z.N. (S.) 768 alternative proposal pending).

Phillips, 1846, (nom. conserv. I.C.Z.N. (S) 768 pending).

Brady, 1876 (pars) (E. bowmani = Involutina lobata Brady, 187=).

Waters, 1928..

Cushman & Waters, 1928.

Rauser-Chernoussova, 1937 (pars).

Rauser-Chernoussova & Reitlinger, 1963 (pars)
Mikhailov, 1939 (E. bowmani of Brady, 1876, non Phillips, 1846 = E. bradyi Mikhailov).
Chernysheva, 1940.
Plummer, 1944 - Cooper, 1947 - Scott, Zeller & Zeller, 1947.
Rauser-Chernoussova, 1948 (pars).
Reitlinger, 1950 - Schlykova, 1951 - Henbest, 1953 - Morozova, 1949 - Grozdilova & Lebedeva, 1954 (pars) - Lipina, 1955 (pars) Brazhnikova, 1956 - Malakhova, 1956, 1957, and 1959 - Ganelina 1956 (pars)
St. Jean, 1957 (pars) - Potievskaya, 1958.
Orlova, 1958 - Durkina 1959 (pars) - Rozovskaya & Henbest, 1962 I.C.Z.N. (S.) 768.
Boghush & Juferev, 1962.
Rozovskaya, 1963.
Loeblich & Tappan, 1964.

Rotalia Hall, 1856 (non Lamarck, 1804)

Involutina Brady, 1870 (pars) (non Terquen, 1862)

Plectogyra Zeller, 1950 and 1957 (pars)
Wray, 1952 - Lehman, 1953 - D.N. Zeller, 1953 - Vdovenko, 1954 - Woodland, 1958.
Okimura, 1958 - Voloshinova & Reitlinger, in Rauser-Chernoussova & Fursenko, 1959 - Boghush & Juferev, 1960 - Lipina, 1960

Miklukho-Maclay, 1960 - Voizekhovskaya, 1961
Schlykova, 1961.

Granuliferella Zeller, 1957 (pars)

Paraplectogyra Okimura, 1958.

Planoendothyra Reitlinger, in Rauser-Chernoussova & Fursenko, 1959.
Boghush & Juferev, 1960 and 1962.
Rozovskaya, 1963.

Plectogyrina Reitlinger, 1959, in Rauser-Chernoussova & Fursenko - Rozovskaya, 1963.

Type Species - Involutina lobata Brady, 1870 = Endothyra bowmani by designation I.C.Z.N. (S.) 768 pending.

Description:

Test free, chambered throughout, plane of coiling changing throughout growth, possibly umbilicate on one side only, partially involute; periphery typically broadly rounded; chambers inflated with asymmetrical apertural face in most stages of growth, with 4 or 5 in first whorl, 5-7 in second whorl, and 6-10 in the third and fourth whorls; aperture basal lunate to semi-:circular slit reflecting asymmetry of apertural face; sutures distinct depressed; septa curved, anteriorly directed; secondary deposits usually well developed, formed in two stages, first the development of the

vestibular ridge, in cross section mound or hook shaped, slightly curved posteriorly across floor of chamber, flattening out in axial ends of chambers, maximum expression in final chamber; second, the development of more extensive basal and sutural deposits, often thickest in earlier chambers; protheca calcareous, dark, finely granular, homogenous, fine pores probably present; proloculum spherical to ovoid.

Ontogeny:

The ontogentic development of Endothyra is usually simple; a spherical proloculum is followed by well developed inflated clearly septate chambers in a plectogyroid coil. In certain species, such as Endothyra baileyi (Hall), however, the proloculum is followed by a number of elongate subtubular chambers with short, anteriorly directed septa (Scott, Zeller & Zeller, 1947, Plate 84, fig.1-11). The form and septation of these chambers is closely similar to that seen in tournayellid genera such as Septabrunsiina or Tournayella and, therefore, suggests a definite phyletic link between Endothyra and this primitive family.

The rotation of the axis of coiling in many cases appears to decrease in the outer whorls, and in some individuals there is evidence that the coiling behaves aberrantly, possibly reacting to stimuli such as cause the remarkable reversal in the direction of coiling in

some individuals of Paramillerella (Plate 8, fig.1). The appearance of 1½-2 whorls apparently planispirally coiled in horizontal axial sections (Grozdilova & Lebedeva 1954 & 1960) does not necessarily indicate that axial rotation has ceased. The width of the tunnel expands rapidly in outer whorls, and it may be wider than the displacement of the angular rotation of the whorl, in such a manner that the mid-point of the tunnel will be displaced only slightly from the plane of the horizontal axial section. The criterion which determines a truly planispiral coil is the condition in which the chambers lose their asymmetrical, evolute-involute form, and embrace the test with uniform prolongation of their axial ends.

The aperture is a simple crescentic slit at the base of the last chamber throughout growth, and in most species the apertural area is modified by a vestibular ridge which does not maintain a constant elevation across the floor of the chamber, but tends to reach a position which is determined by the height of the apertural arch (cf. Text fig.4A, B, & C). As the aperture is asymmetrical, and the contour of the floor of the chamber may vary depending on the attitude of the coil at any particular growth stage, it is possible to produce considerable variation in cross sectional appearance of the vestibular ridge within a single

specimen or species. The basal deposits of juvenile individuals are usually thinner than the juvenile stages of an adult specimen, and in some species the vestibular ridges are poorly developed in the juvenile individuals as compared with the adults.

The morphological expression of dimorphism in this genus is not fully understood at present. It has been suggested by Henbest (1953 p.64) that the dimorphism is expressed in the variation of the degree of axial rotation, and that there is a range from planispiral to plectogyroid forms. Although this relationship has not been substantiated it could have limited applicability in some populations of Meramecian age. At other horizons, however, dimorphic variation in axial rotation, if present, is of more moderate proportions.

It has been stated by Rozovskaya (1963 p.33) that species of Endothyra determined on external form, oblique, or horizontal axial sections only are invalid. Clearly species described only on external form require revision, and it is true that species described only on a single section, or on sections of one particular type, are rather unsatisfactory. It is, however, a little surprising to find species based on a number of well centred horizontal axial sections invalidated while a vast number of species based on a variety of imprecise

sections are accorded validity. Vertical axial sections or near vertical axial sections are no more satisfactory in determining the characters of Endothyra than the complementary section, and the addition of another poorly orientated section will not necessarily help to define the biocharacters of the species. From Zeller's excellent exposition of the structure of of Endothyra, and from the results of the present study, it is clear that centred horizontal axial sections are most valuable for taxonomic purposes, (cf. Text, figs.4A-C), since they reveal the nature and development of the basal deposits while giving some indication of the degree of axial rotation together with details of the chambers and septa. Ideally a transverse section should also be given, (Text, fig.4G) however, since there is no unambiguous morphological guide to the location of this plane of section, its selection is largely a matter of chance, and vertical axial sections must be relied on in most cases.

At least two thirds of Russian descriptions of Endothyra give no detailed account of the character of the secondary deposits, and it is apparent that little importance is attached to this particular biocharacter. The characters which Russian authors (Rauser-Chernoussova, 1948, Reitlinger, 1950, Grozdilova & Lebedeva, 1954, Rozovskaya, 1963, etc.)

TEXT - FIGURE 4.

Endothyra phrissa (D.N. Zeller), reconstruction based on serial sections, X100 approx. (stippled protheca: black epitheca).

1-3. apertural and lateral views.

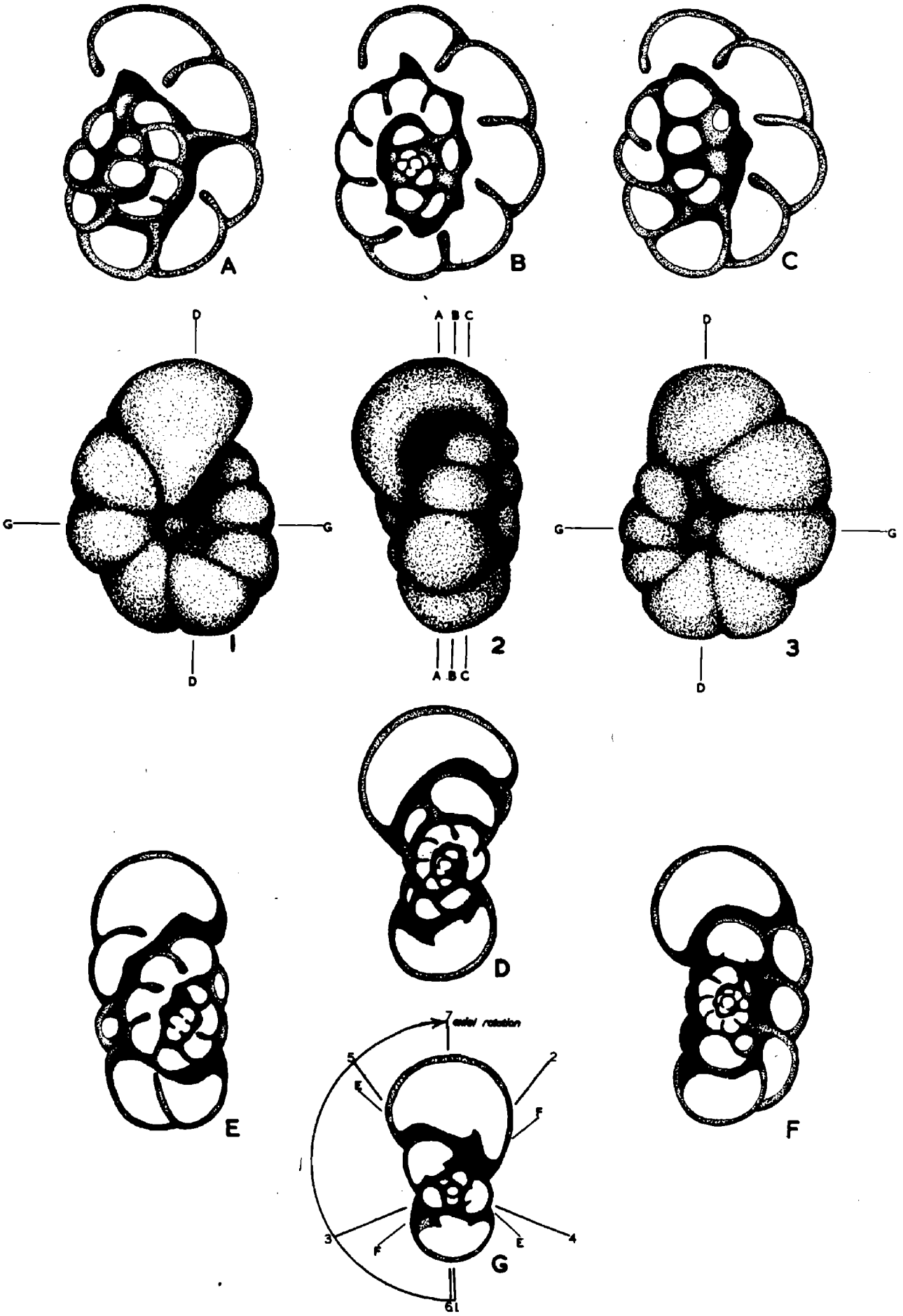
A-C. horizontal axial section and parallel horizontal sections showing variation in apertural height and in the development of the vestibular hook.

D. vertical axial section.

E. horizontal axial section in penultimate whorl.

F. horizontal axial section in first whorl.

G. transverse section showing the positions of each half whorl and thereby the axial rotation of 180 degrees.


A
B
C
D
G
G
1
D
A B C
2
A B C
D
G
G
3
D
D
E
D
F
7
axial rotation
5
E
2
F
3
F
E
4
G
G1

consider significant are those displayed most clearly in axial sections, such as, ratio of axial length to diameter, character of the umbilicus, degree of involution of whorls, and character of the peripheral margin. Although some of these characters are obviously of importance, most of them, in detail, subject to gross variation resulting from the changing external morphology of the test during growth. This is illustrated in Text fig.5, in which the changing aspect of the test is reconstructed as successive chambers are removed.

Comparison and Affinities:

Recently the name of this genus has become the centre of considerable controversy, and is at present the subject of a petition to the International Commission on Zoological Nomenclature, the result of which is pending.

The history of this particular taxonomic muddle is that Brown (1843, p.17, Pl.6, fig.2), gave the first description and figure of Endothyra bowmani, but, although he attributed the authorship to Phillips, it is clear that he alone was responsible for its indication, definition, or description. Thus contrary to St. Jean (1957 & 1962, p.402) Brown, (1843) has priority over all other references to Endothyra.

Phillips later (1846, p.17, fig.1) published his

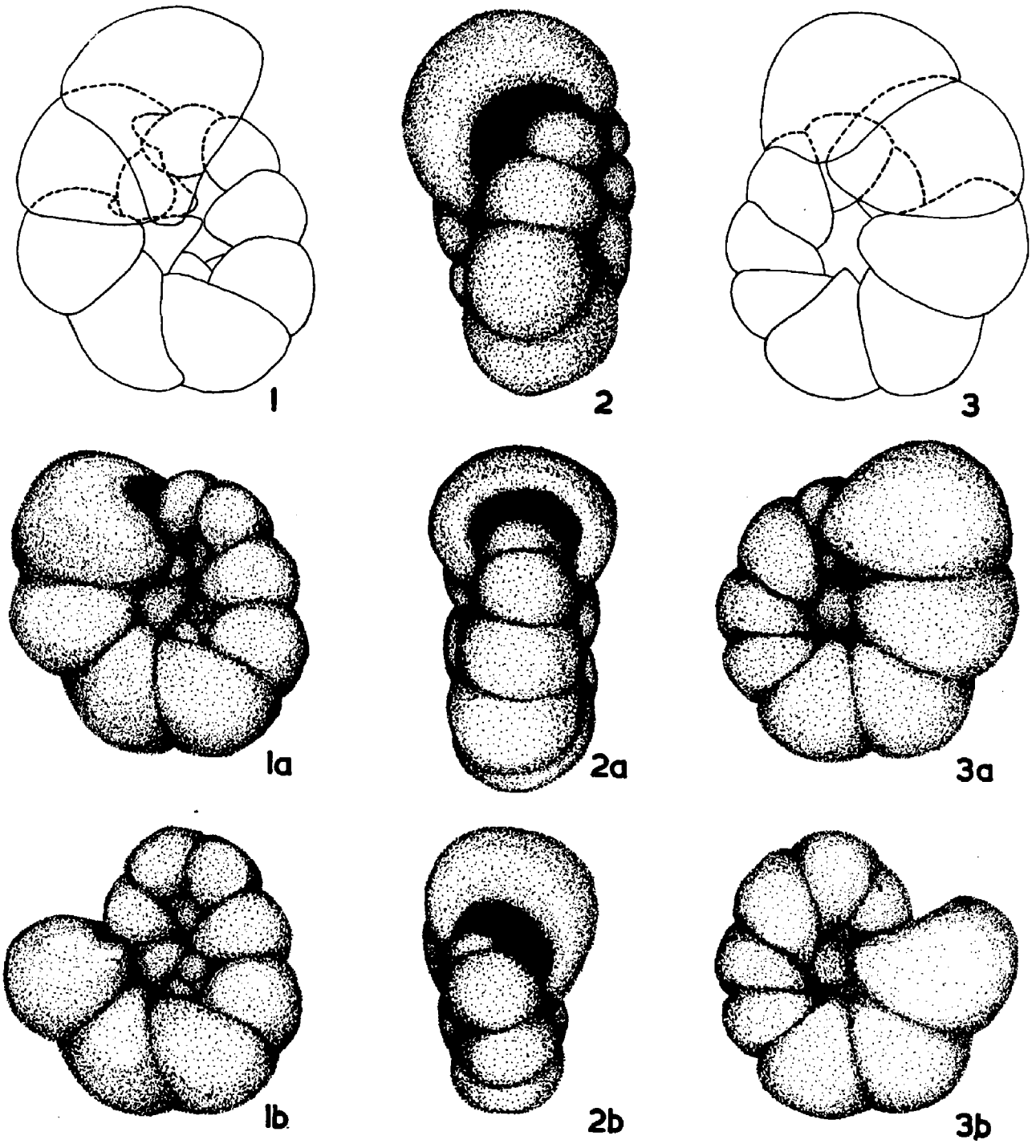
TEXT - FIGURE 5.

Endothyra phrissa (D.N. Zeller), reconstruction of the external form of the test with the subtraction of successive chambers and illustrating the manner in which chamber form and apertural shape are controlled by plectogyral mode of coiling, X125 approx.

1-1b. lateral view.

2-2b. apertural view showing clearly varying form of the aperture, and alternating involution and evolution of chambers on opposite sides of the test.

3-3b. opposite lateral view.


1
2
3
1a
2a
3a
1b
2b
3b

own description of Endothyra bowmani with a figure which differed radically from that of Brown. In his monograph, Brady (1876 p.29,93) with a broader understanding of Endothyra than would be accepted at present, and unaware of the description by Brown (1843), took E. bowmani Phillips as the type of genus. Brady realised the inadequacies of Phillips' figure and description, but suggested that it must be taken for what it was worth. It is apparent that, as first reviser, Brady had no knowledge of Phillips's type specimens; a fact which is apparent from his comments on p.14 of the monograph. Indeed, it is probable that Phillip's material had already been lost at this time for a large part of his collection was destroyed during his lifetime (see Sherborn 1940 p.107). Thus Brady's judgement, based solely on the figure, is of no greater significance than that of any later worker, and it is entirely speculative to suggest, as Loeblich & Tappan (1963 p.283), that the highly stylised drawing of Phillips is conspecific with the specimens of Brady. Furthermore, Brady's uncritical approach to this question is emphasised by the fact that he included Rotalia baileyi Hall as a synonym of E. bowmani, and examination of Brady's collection in the British Museum Natural History reveals that many of his specimens referred to E. bowmani are not conspecific with his

figured specimens. As much may be inferred from the fact that in Brady's distribution charts E. bowmani ranges throughout the Carboniferous. Clearly his concept of this species was sufficiently broad to encompass the modern genus.

Although Mikhailov (1939) is considered correct in his view that Brady's specimens are not conspecific with E. bowmani Phillips, it is equally apparent from comparison of Brady's material with the figures of E. bradyi Mikhailov that these specimens cannot be regarded as conspecific. There is, therefore, no basis for the recognition of E. bradyi Mikhailov, 1939, as the type of Endothyra as has been proposed by Rosovskaya (1962).

The type of Phillips without adequate description or figure, and most seriously without type specimens or locality, is clearly a nomen dubium. Furthermore, as a junior homonym of E. bowmani Brown it ceases to have availability and, therefore, its designation by Brady (1876) was invalid. Consequently Brady's specimens (Pl.V. figs.1, 2a, 2b, and 4) should be referred to the nominal special Involutina lobata Brady, (1870), a taxon which was validated by the following published description of this date:

> Involutina lobata sp.nov. test lenticular, rotalian, lower surface sometimes concave,

periphery rounded; chambers ventricose; septa constricted.

Normal application of the rules of nomenclature leads to the recognition of E. bowmani Brown, 1843 as the type of the monotypic genus Endothyra, and therefore, the crux of the debate concerning this genus centres on the clarity with which Brown's description and figure can be interpreted. The description is not sufficiently definitive for modern taxonomic work, and the figure is an artistic impression. However, if the figure is interpreted, as strictly as its limitations allow, it is clear that is is planispiral, and that it can be variously interpreted as having from 7 to 10 chambers in the first whorl, with 15 or 16 in the second, 16 in the third, and 18 in the fourth whorl. The radially directed septa are normal to the spiral wall, which is without lobulation. The character of the wall and secondary deposits are, of course, unknown. The opinion of Zeller & Zeller (1962) and St. Jean (1962), that the neotype of D.E.N. Zeller (1962) is identical with Brown's figure is disputed. The specimen is incorrectly described by D.E.N. Zeller (1962) such that in the count of the chambers the asymmetry of the first whorl has been ignored. The count is not from the first chamber, which is isolated with the proloculum from the planispiral part of the

test, but probably from the fourth chamber. Thus the first whorl in all probability has 4 or 5 chambers, and the second whorl 9, which is entirely characteristic of planispiral specimens of the Lower to Middle Visean. Brown's figure has the characters of a sagittal section of a relatively advanced fusulinid, and it is believed that these cannot be duplicated in a specimen of Middle or Upper Visean age (i.e. Mountain Limestone). This conviction is based on research on populations of Paramillerella and Pseudoendothyra in which over 1,000 specimens were examined in sagittal section. This revealed not a single specimen even remotely approaching Brown's figure in terms of chamber count.

It is, therefore, concluded that since Endothyra Brown, 1843, cannot be literally interpreted but must be treated arbitrarily, it is more convenient to conserve the traditional usage of the name in the sense of Brady (1876). Consequently the generic name Endothyra Brown, 1843 is here interpreted with reference to the type species Involutina lobata Brady, 1870.

The plectogyral nature of the coiling was regarded as the most fundamental characteristic of this genus by Zeller (1950 and 1957), nevertheless, it is apparent that many of the specimens assigned to Plectogyra by Zeller show primitive characters of septation and chambering, and should be referred to genera of the family Tournayellidae.

Paraplectogyra cannot be differentiated from Endothyra on the basis of its three layered, fusulinellid, wall structure which has already been described in the latter genus by Scott, Zeller & Zeller (1947 p.558). In any case, it is not clear at present how far the 'fusulinellid structure' reflects the primary structure of the wall, or is the result of diagenetic changes in the host sediment.

Endothyranella can be distinguished from Endothyra by its highly arched sub-circular aperture, which appears at the more evolute stage of growth prior to the appearance of the characteristic rectilinear phase (cf. St. Jean 1957, Pl.1, fig.10-12, Pl.2, fig.1-2).

The characters of the genus Plectogyrina are not clear, Reitlinger (1959 in Rauser-Chernoussova & Fursenko), and Rozovskaya (1963) suggest that the early whorls are coiled in a plane at above 90 degrees to the last whorl. This, however, is not obvious in the type species, and in the figured type (1959, Pl.V. fig.12) it is quite clear that the last whorl is not at an angle of 90 degrees to the penultimate whorl, nor, indeed, the earlier whorls, one of which lies in a plane similar to the outer whorl. The characters attributed to this form appear to result from misunderstanding of the character and morphology of the plectogyroid coil, and this is accentuated by attempts to study specimens in

oblique unorientated sections. It is significant that not a single specimen of this supposed genus has yet been figured in a centred horizontal axial section, and in this respect its relationship to Mediocris requires study (cf. p.73).

Reitlinger (1959 p.149 in Rauser-Chernoussova & Fursenko) separated Planoendothyra from Endothyra on the basis of its secondary deposits, which are heavy and well developed in the lateral portion of the chambers. The type species Endothyra aljutovica Reitlinger, 1950 is a plectogyroid form with a low axial rotation, and it cannot be regarded as planispiral as is suggested by Rozovskaya (1963 p.60), for the asymmetry of the chambers and coiling is striking even in the final whorl. A distinctive trend in Endothyra of the Middle Carboniferous is the tendency to produce very heavy basal deposits (cf. Zeller, 1950 p.20). This eventually results in forms whose vestibular ridges are swamped by the thick basal layer. Typical specimens have been figured by Zeller (1950 p.21, Pl.5, fig.1-3 &5) and, although Endothyra aljutovica has not been figured in a true horizontal axial section, it appears to be a form typical of this lineage. Certainly its characters do not warrant the congeneric or familial relationship with Quasiendothyra suggested by Loeblich & Tappan (1964 p.346) and Rozovskaya (1963 p.60).

Preservation and Matrix:

Material extracted from shales tends to have lost part of all of the wall in the outer whorls, and partial steinkerns often give the impression of having limbate sutures. Compaction in shales causes widespread distortion, crushing, and collapse of the chambers of Endothyra, especially in the final whorl. (Pl.10, fig.7,8). In limestones the effects of compaction are generally much less pronounced. D.N. Zeller (1953) considered the occurrence of angular distorted chambers to be of specific significance and apparently took this condition to be a primary growth feature. It is possible that a species with a fragile test may appear more frequently in a distorted condition, but collapse of the chambers is far more commonly a feature of the lithology than of the species.

The diaphanotheca of Endothyra baileyi was said to have a fine alveolar structure by Scott, Zeller & Zeller (1947 p.558). In a later assessment Zeller (1950 p.4) regarded the transverse alveoli, or pore canals, as the result of the alignment of crystal granules, possibly as a result of recrystallisation. This is essentially a return to the interpretation of Henbest (1931) which may well be correct in this instance (see p.25). However, the description by Skinner & Wilde (1954 Pl.49, fig.3) of Millerella

with pores infilled by iron ore, has shown that the thin homogeneous finely granular type of wall, hitherto regarded as imperforate, probably has fine pores which are not readily visible under normal conditions of preservation. It is possible, therefore, that in a well preserved wall it may by possible to accept regular, light or dark, fine transverse discontinuities as evidence of pores. (cf. St. Jean, 1957 and Reitlinger, 1950).

The extent to which the layering of the wall of Endothyra has been influenced by the diagenesis and lithification of the host sediment is not entirely clear. All the material examined from the Upper Limestone Group has a simple homogeneous primary wall without a tectum and, in many cases, the preservation is such that the homogeneity and extreme fineness of grain size in the wall precludes any suggestion that the layering may have been destroyed by redistribution. Indeed, it has been noted in some instances that recrystallisation and replacement of the wall, together with iron enrichment, may give it a specious layering (Plate 3, fig.4, & Plate 5).

In general the wall of Endothyra appears quite resistant to the effects of recrystallisation and dolomitisation, and it survives in limestones where most other elements of the foraminiferal fauna have been obliterated.

ENDOTHYRA PHRISSA D.N.Zeller.

Plate 9, fig.1-6 & 9.

Plectogyra phrissa D.N. Zeller, 1953, p.198,
Pl.28, fig.1,4,6.

Endothyra tortilis St. Jean, 1957, p.28
Pl.1, fig.4-6.

Endothyra kennethi St. Jean, 1957, p.28,
Pl.1, fig.7-8.

Description:

Test free, discoidal with very broadly rounded periphery, coiled in a plectogyroid spiral with a high axial rotation, strongly umbilicate on one side only, with five chambers in the first whorl, 6 or 7 in the second whorl, and 6-8, usually seven, in later whorls; chambers globular, highly inflated, having an asymmetri-:cal but sub-circular cross section; sutures distinct and depressed throughout; peripheral margin strongly lobulate; septa long, strongly arcuate, forming continuous smooth curve with the outer wall, with thin secondary deposits on the posterior surface above the tunnel; protheca slender (10-15 microns), dark, homogeneous, finely granular, possibly with fine pores; secondary deposits well developed; vestibular ridges reaching a maximum in last chamber, prominent also in earlier chambers, in cross section distinctly

asymmetrical, anteriorly directed, sharp, wedgelike, decreasing in size and becoming more rounded in earlier chambers; sutural and basal deposits often thin or absent in last chambers, usually well developed in earlier whorls; aperture low asymmetrical lunate slit at base of last chamber; proloculum spherical, about 30-40 microns.

Dimensions:

Specimen Pl.9, fig.1 - Maximum diameter, 0.62 mm. Thickness of wall in last whorl - 0.012 mm. Thickness of wall in penultimate whorl - 0.010 mm. Specimen Pl.9, fig.2 - Maximum diameter, 0.50 mm. Thickness of wall in last whorl - 0.010 mm. Specimen Pl.9, fig.3 - Maximum diameter, 0.51 mm. Maximum width, 0.28 m.m. Thickness of wall in last whorl - 0.013 m.m.

Depository:

Hunterian Museum of the University of Glasgow on slides Nos. P.432/1-4, from shales three inches above the Orchard Limestone, Upper Limestone Group, Namurian, in River Avon at Strutherhill, Larkhall, Lanarkshire.

Comparison and Affinities:

This species is distinctive in its large, slender walled, inflated chambers, with strongly arcuate septa, and in its prominent anteriorly directed vestibular

ridges. It is apparently closely related to Endothyra bradyi Mikhailov, and, indeed may be regarded as synonymous with E. bradyi of Voloshinova & Reitlinger (1959 Pl.V. fig.11, in Rauser-Chernoussova & Fursenko) but the characters of E. bradyi sensu-stricto are difficult to determine. The original figures of Mikhailov (1934 Pl.4, fig.1,2) do not disclose the character of the basal deposits, and descriptions of subsequent authors, such as Rauser-Chernoussova (1948 p.176) and Grozdilova & Lebedeva (1954 p.108, & 1960 p.65), place an emphasis on characters which in themselves are not regarded as having fundamental significance. Moreover, with the numerous subspecies which have been proposed the characters of E. bradyi are so broad that they would embrace nearly all Upper Visean and Namurian species.

Endothyra phrissa resembles Endothyra lobata (Brady) in basic shell architecture but differs strikingly in the development of prominent wedge-like vestibular ridges and in its more slender wall. The species Endothyra kennethi and E. tortilis, which were described from a single shale horizon by St. Jean (1957, p.27-28), are regarded as synonyms for they were differentiated on external morphology. St. Jean completely failed to appreciate the nature of the plectogyroid spiral and its resultant, the changing

aspect of the final whorl during growth (cf. Text fig.5). Both forms appear to be identical to E. phrissa in all their major characters, in particular, slender wall, inflated chambers and characteristic basal deposits.

Preservation and Matrix:

The figured specimens extracted from calcareous shales now show an irregular loss of the external wall. The tendency of these tests to leave internal moulds may be related to the fact that the chambers are commonly infilled, not by drusy calcite, but by finely granular calcium phosphate (cf. Pl.8, fig.5) which would tend to facilitate differential weathering. Although a detailed petrographic study has not been attempted, the phosphate appears to form a primary infilling, and it has been noted so far only in material obtained from shale horizons. Material from limestones show the typical drusy calcite infilling.

Horizon and Facies:

Originally recorded by D.N. Zeller (1953) from the Kinkaid Limestone, Chesterian, Mississippian, and ranging into the Pennsylvanian of the United States (St. Jean, 1957), this would appear to be a character-istic Namurian species. It occurs throughout the Upper Limestone Group, being rare in the lowermost, Index Limestons, but reaching a widespread and

exclusive distribution in the limestones and shales of the Orchard and Calmy positions.

ENDOTHYRA BARBATA sp. nov.

Plate 9, fig.7-8 & 10-13.

Endothyra bradyi Mikhailov, var. bradyi
Mikhailov - Grozdilova & Lebedeva,
1954 (pars) p.108, Pl.XII, fig.6.

Description:

Test free, discoidal with broadly rounded periphery, coiled in a plectogyroid spiral with axial ratio decreasing rapidly and very low in outer whorls, asymmetrically biumbilicate, partially involute but becoming more evolute in outer whorls, with 5 chambers in the first whorl, 6 or 7 in the second, and 7 or 8, usually 8, in the later whorls; chambers strongly inflated having an asymmetrical but sub-circular cross section; sutures distinct and depressed throughout; peripheral margin lobulate; septa slender, slightly differentiated from the spiral wall, anteriorly directed, straight to slightly curved, often with secondary thickening on posterior surface above the tunnel; protheca slender (8-20 microns), dark, homogeneous, finely granular, possibly with fine pores; secondary deposits well developed, with thick prominent basal layer extending into axial ends of chambers, sutural deposits in small triangular wedges at the intercameral suture;

vestibular ridges culminating in sharp wedge like anteriorly directed ridge in final chamber, reduced to low mould like ridges in most earlier chambers, aperture asymmetrical lunate slit at base of last chamber; proloculum spherical, diameter about 30 microns.

Dimensions:

Holotype Pl.9, fig.7.

Maximum Diameter, 0.67 mm.

Thickness of protheca in last whorl - 0.021 mm.

Thickness of protheca in penultimate whorl - 0.012 mm.

Paratype Pl.9, fig. 8.

Maximum Diameter, 0.66 mm.

Maximum Width, 0.030 mm.

Depository:

Hunterian Museum of the University of Glasgow on slides Nos. P.433/1-2, from the Plean Limestone position, Upper Limestone Group, Namurian, of Craigburn, Uddington, nr. Douglas, Lanarkshire.

Comparison and Affinities:

This is a form which Grozdilova & Lebedeva (1954) regarded as very closely related to E. bradyi, var. bradyi Mikhailov, although Rozovskaya (1963 p.42) did not accept this relationship, and it is, in any case, clear that E. barbata can be distinguished from the majority of its contemporary species by its very low

axial rotation. It may be closely related to the specimen figured by Zeller (1950 Pl.5, fig.5) from the Middle Pennsylvanian but appears to have a thinner basal layer with more distinctive vestibular ridges. E. barbata is similar to E. aljutovica Reitlinger in its low axial rotation and rather evolute coiling, but it can be differentiated from the latter form by its fewer and more inflated chambers in the final whorl, and by rather thinner secondary deposits with distinct vestibular ridges.

Horizon and Facies:

This species first appears abundantly in the Plean No.1 Limestone, and is a common and characteristic form in the Castlecary Limestone, Upper Limestone Group, Namurian of Scotland. It occurs in a wide variety of facies from bioclastic micrites to calcareous bioclastic shales.

ENDOTHYRA PANDORAE D.N. Zeller, 1953.

Plate 10, fig.1-8.

Plectogyra pandorae D.N. Zeller, 1953, p.196, Pl.28, fig.7.10.13. & 14.

Description:

Test free, discoidal with broadly rounded periphery, partially involute, coiled in a plectogyroid spiral with medium axial rotation, with 5 chambers in the first whorl, 6 or 7 in the second, and 8-10 in later whorls, final whorl of mature individuals typically with 8 or 9 closely set moderately inflated chambers; umbilicus broad and shallow on one side, narrower and deeper on opposite side; sutures slightly depressed; peripheral margin faintly lobulate in early stages, becoming more prominent in later stages of large specimens; septa long, straight or slightly curved, differentiated from spiral wall by sharp downward curve, the apertural face being almost flat; secondary deposits form moderately thick basal deposit, extending into axial ends of chambers where vestibular ridge degenerates, and secondary material extends up posterior and anterior faces of septa forming thickened margins on the septal ends over the tunnel, small sutural wedges of secondary material occur at the intercameral sutures; vestibular

ridges feeble in juvenile individuals (diam. less than 0.35 mm.) and poorly developed in most adult specimens, may become fairly prominent in specimens greater than 0.5 mm., in horizontal axial section forming low mounds, sometimes asymmetrical with steeper anterior surface; protheca relatively thick (15-25 microns), homogeneous, finely granular, with fine transverse structure in some specimens, aperture low slit at base of final chamber reflecting the asymmetry of the apertural face; proloculum spherical, about 35 microns in diameter.

Dimensions:

Specimen No.P.436.

Maximum Diameter, 0.51 mm.

Thickness of wall in final whorl - 0.014 mm.

Thickness of wall in penultimate whorl - 0.011 mm.

Specimen No.P.437/1.

Maximum Diameter, 0.61 mm.

Thickness of wall in final whorl - 0.015 mm.

Thickness of wall in penultimate whorl - 0.012 mm.

Specimen No.P.437/2.

Maximum Diameter, 0.38 mm.

Maximum Width, 0.22 m.m.

Thickness of wall in final whorl - 0.018 mm.

Maximum Diameter, 1st whorl, 0.11

Thickness of wall in 1st whorl - 0.0006

Specimen No.P.438/1.

Maximum Diameter, 0.54.

Thickness of wall in final whorl - 0.019.

Thickness of wall in penultimate whorl - 0.012.

Specimen No.P.438/2.

Maximum Diameter, 0.67.

Thickness of wall in final whorl - 0.023.

Thickness of wall in penultimate whorl - 0.014

Specimen No.P.439

Maximum Diameter, 0.74.

Thickness of wall in final whorl - 0.022.

Thickness of wall in penultimate whorl - 0.017.

Depository:

Hunterian Museum of the University of Glasgow, type No.P.436 from Lyoncross Limestone, Overlee, Clarkston, Renfrewshire; types No.P.437/1-2 from Index Limestone, Poniel Water, Coalburn, Lanarkshire; types Nos.P.438/1-2 from Lyoncross Limestone, Craigburn, Uddington, nr. Douglas, Lanarkshire; and type No.P.439 from Index Limestone, Kennox Water, nr. Douglas, Lanarkshire; all from Upper Limestone Group, Namurian of Scotland.

Comparison and Affinities:

This species is closely similar to Endothyra lobata (Brady), but can be differentiated by its lower

axial rotation, greater number of less inflated chambers with the septa differentiated from the spiral wall. It is also very similar to E. paucinodosa sp. nov. but can be distinguished by the less inflated and more numerous chambers and the much more extensive secondary deposits, and can be distinguished from E. barbata sp.nov. by its less conspicuous moundlike ridges, less inflated chambers, and stouter wall.

This form shows some resemblance to species of the groups E. mosquensis and E. aljutovica of Reitlinger (1950 p.30). However, E. pandorae, although sometimes approaching E. aljutovica in chamber form, has a much more involute test and a greater axial rotation. Of the species of the group E. mosquensis, E. rzhevica appears to be very closely similar to E. pandorae but can not be directly compared because the basal deposits have not been described, while E. bradyi var. compressa Reitlinger has more inflated chambers and more prominent vestibular ridges. E. mosquensis itself appears to differ in having fewer and more inflated chambers, and, possibly, in having more prominent vestibular ridges similar to E. bradyi.

Preservation and Matrix:

Crushing and collapse of the chambers are a relatively common feature of this species. Some of the specimens with collapsed and distorted chambers

such as those in Plate 10, figs.7, 8, are closely similar to E. versabilis D.N. Zeller, although they do have somewhat thinner basal deposits. This suggests that the diagnosis of E. versabilis primarily on the irregularity of chamber form is ill-founded, and it is considered that the holotype (Plate 28, fig.18) should be referred to the species E. kentuckyensis while the paratype (Plate 28, fig.2) may be compared with E. pandorae.

The wall structure is typically well preserved despite the fact that, in some cases, the host sediment has undergone a considerable degree of alteration through redistribution and replacement. Although relatively thick, the protheca is so finely granular and uniform that it shows no evidence of ever having been differentiated. In a number of specimens the protheca both externally and internally has a very thin dark selvage, but, in most cases, this appears to be simply the contact between the protheca and the adjoining medium - the matrix, drusy infilling, or epitheca. In most cases the dark zone of the wall is no more prominent than the boundaries between large crystals of the drusy infilling. Moreover, just as is the case in the drusy infilling, the interfaces of the crystals provide a route for permeating solutions and, as a result, commonly

become stained by oxides and sulphides of iron. Since the foraminiferal wall is commonly the site of active iron enrichment, presumably due to its residue of organic material coating the walls and infiltrating the pores, it is considered that a major cause of the opacity of the boundaries is staining by sulphides and oxides of iron. (cf. Plate 5, fig.1.).

Horizon and Facies:

Occurring abundantly in the Lyoncross and Index Limestones, the lowermost marine horizons of the Upper Limestone Group, where it has been found in both limestone and calcareous shale facies. In the Index Limestone E. pandorae occurs in association with rare specimens of E. paucinodosa sp.nov. and more common, but not abundant, E. phrissa. E. pandorae most characteristically develops 9 or 10 chambers in the last whorl of mature individuals in the Index Limestone, but in the Lyoncross Limestone, where it occurs in association with rarer specimens of E. phrissa, it develops only 8 or 9 chambers in the last whorl. Study of the populations from a number of localities suggests that the two horizons may actually be differentiated on the basis of the chambers occurring in the last whorl of mature specimens. (see p.351 and Text figs.27-29).

ENDOTHYRA PAUCINODOSA sp. nov.

Plate 10. Fig.9.

Description:

Test free, discoidal with broadly rounded periphery, coiled in a plectogyroid spiral and with low axial rotation, asymmetrically biumbilicate, the last whorl in mature individuals containing 7, or more rarely 8, large strongly inflated chambers with distinctly asymmetrical axial section; sutures distinct, depressed throughout; peripheral margin strongly lobulate; septa straight to slightly curved, sometimes showing slight differentiation from the spiral wall, with sporadic thin secondary thickening on posterior surface above tunnel; protheca thin (13 microns), dark, homogeneous, finely granular, possibly with fine pores; secondary deposits very poorly developed, basal layer absent throughout most of the test, sutural deposits thin indefinite; vestibular ridges irregularly developed, low, symmetrical, moundlike in horizontal axial section; aperture lunate slit at base of final chamber reflecting asymmetry of apertural face; proloculum spherical, about 30 microns in diameter.

Dimensions:

Holotype Plate 10, fig.9.

Maximum Diameter, 0.059 mm.

Thickness of wall in last whorl - 0.01. mm.

Thickness of wall in penultimate whorl - 0.010 mm.

Depository:

Hunterian Museum of the University of Glasgow on slide No.P.434/1 holotype, from Index Limestone, Upper Limestone Group, Namurian, of Kennox Water, nr. Douglas, Lanarkshire, and paratype No.P.435 from Index Limestone, at Auldhouse Burn, Muirkirk, Ayrshire.

Comparison and Affinities:

This species may represent an extreme stage in the variation of populations of Endothyra pandorae D.N. Zeller, but it is separated on the grounds that it has fewer and more highly inflated chambers with extremely sparse secondary deposits. It can be differentiated from E. lobata (Brady) by its lower axial rotation and very much thinner secondary deposits with sporadic vestibular ridges, and from E. tantala D.N. Zeller, by the absence of prominent hook like ridge in the final chamber together with the overall paucity of secondary material.

Horizon and Facies:

A rare form found so far only in the Index Limestone at the base of the Upper Limestone Group, where it occurs in both limestones and calcareous shales.

ZELLERELLA gen. nov.

Endothyra Zeller 1950 and 1957 (non Endothyra Brown, 1843)
Wray, 1953.
Lebedeva, 1954 (pars)
Lipina, 1955 (pars).
Woodland, 1958 - Armstrong, 1958.
Voizekhovskaya, 1961 (pars).
Loeblich & Tappan, 1964 (pars).

Parastaffella Grozdilova in Lebedeva, 1954.
Lebedeva, 1954.

Paramillerella Anisgard & Campau, 1964.

Eostaffella Rozovskaya, 1963 (pars).

Type Species:

Paramillerella thompsoni Anisgard & Campau, 1963, p.102, Plate 9, fig.7.

Description:

Test free, chambered throughout, discoidal or nautiloid to ovoid, involute, biumbilicate, planispirally coiled, but with some axial rotation of the initial whorl, typically with 4 to 5 chambers in the first whorl, 7 or 8 in the second, 9 or 10 in the third, 9 to 13 in the fourth, and 10 to 14 in the fifth; periphery well rounded; umbilicus typically shallow;

chambers inflated, width greater than height in all whorls, ratio greater than 1 throughout growth; sutures depressed; septa rather short, strongly anteriorly directed, curved running smoothly into spiral wall; secondary deposits present, prominent slender, anteriorly directed hook in final chamber, thin basal and sutural deposits; protheca thick calcareous, dark, finely granular, homogeneous, with fine transverse pores; aperture low slit at base of final chamber, greatly reduced or closed by secondary material in some cases.

Ontogeny:

Immediately following the proloculum of a number of species of this genus are a number of very long chambers (width/height ratio 3) and these show the type of septation characteristic of the tournayellids. (cf. Zeller, 1950, Plate 2, fig.2, Plate 3, fig.3, and Plate 4, fig.3). That is to say the septa are short and strongly anteriorly directed, forming a smooth sweeping curve with the spiral wall. In later whorls these primitive characters become progressively eliminated; the chambers become narrower and higher while the septa increase in length, are not so strongly anteriorly directed, and begin to show an incipient differentiation from the spiral wall. Conventional

interpretation of these ontogenetic characters intimates that Zellerella may have evolved from a tournayellid ancestor, but the phylogeny of these forms may be more complex. Morphologically Zellerella is closely similar to Endothyra, particularly species of the type of Endothyra baileyi (Hall), and it has been suggested by Henbest (1953 p.64) that the relationship is one of dimorphism; planispiral forms supposedly forming a percentage of all plectogyroid populations. This relationship, however, has not been substantiated with regard to the dimensions of the proloculum, and populations consisting entirely of planispiral forms are known. (Anisgard & Campau, 1963). The marked morphological similarity of the two forms does, indeed, suggest a close phyletic link which may have been expressed initially in a dimorphic relationship in some populations but, on the other hand, there is, as yet, no evidence to refute the possibility that they developed independantly from planispiral and plectogyroid tournayellid ancestors.

Comparison and Affinities:

Species which are here referred to Zellerella gen. nov. were initially assigned to Endothyra by Zeller (1950) mainly on the grounds that they were planispiral and, therefore, bore a vague resemblance

to Brown's original figure of Endothyra bowmani. Such a course was expedient for it provided a type which could be regarded as distinct from both Plectogyra and the recognised primitive fusuline genera Paramillerella and Eostaffella. This interpretation is invalidated, however, by the pending I.C.Z.N. petition (Z.N. (S.) 768), which requests the recognition of Endothyra as interpreted by Brady (1876). In arguing the case for plectogyroid Endothyra, Henbest (1953 and 1962) emphasised the dimorphic nature of planispiral forms as has been discussed above, but the established occurrence of wholly planispiral populations effectively invalidates this view. Thus Zellerella is considered to be distinct from Endothyra Brown (as interpreted by Brady) by virtue of its planispiral coiling.

The type species of this genus was refered to Paramillerella on its original description by Amisgard & Campau, (1963), on the grounds that it had a three layered wall, a tunnel bordered by chomata, and an infrequently developed, or vestigial, aperture. This interpretation, however, is disputed on a number of grounds. The wall structure is not a diagnositc criterion, and the structures described are common to Endothyra and Paramillerella. The recognition of chomata in Zellerella thompsoni is based on a

misinterpretation of morphology in random sections. In the sense strictly applied in this study, and as they are typically developed in fusulinids, chomata are levee like bodies running parallel to the tunnel distinctly modifying the periphery of the previous whorl to form a platform or channel like form in the inter-:septal area. The mere thickening of the septal ends adjacent to the tunnel does not constitute chomata, and it is held that it would be morphologically and functionally contradictory to find vestibular hooks and chomata in the same specimen. In the discussion of secondary deposits (p.32) the differences in the character of the deposits are regarded as the expression of differing conditions of cytoplasmic organisation and function, and so it is considered that the presence of a hook in two thirds of the specimens examined by Anisgard & Campau (1963 p.99) unquestionably indicates a close relationship with the endothyrids. The aperture does not provide a criterion by which Endothyrinae and Ozawainellinae may be distinguished for it is now known to be present in the established primitive endothyracean, Pseudoendothyra, (Plate 18, fig.1,3), Paramillerella, (Plate 2, fig.5: Plate 14, fig.1: Plate 15, fig.13: Plate 16, fig.1 & Plate 17, fig.4) and Millerella (cf. Moore, 1964 p.296). It is, therefore, considered that Zellerella can be distinguished from Eostaffella,

and Paramillerella by the primitive inflated form of the chambers, with the width greater than the height, strongly anteriorly directed septa, and prominent vestibular hooks in the last chamber of most specimens. Zellerella slightly resembles Globoendothyra but can be distinguished by the simpler wall structure and the essentially planispiral coiling of the test.

Horizon and Facies:

Zellerella has a widespread occurrence in the Mississippian of the United States where it is a characteristic form in strata of Meramecian age. It has been recorded abundantly in the Lower and Middle Visean limestones of Great Britain (Cummings, 1961) but does not appear to be a common form in the U.S.S.R. where a few records suggest its occurrence in strata of Upper Tournaisian and Lower Visean age. (Lipina, 1955, Voizekhovskaya, 1961 and Grozdilova & Lebedeva, 1954).

Previously Described Species:

The following species are considered to be referable to this genus:

Zellerella disca (Zeller). 1956.
" ermakiensis (Lebedeva), 1954.
" finitima (Voizekovskaya), 1961
" ingrata (Lebedeva), 1954
" juliusi (Voizekhovskaya), 1961

Zellerella macra (Zeller), 1957.

" originis (Voizekhovskaya), 1961.

" prodigiosa (Armstrong), 1958.

" pressa (Grozdilova), in Lebedeva, 1954.

" rara (Grozdilova), in Lebedeva, 1954.

" rotayi (Lebedeva), 1954.

" spiroides (Zeller), 1957.

" symmetrica (Zeller), 1957 (= Endothyra scitula Toomey, 1961).

" thompsoni (Anisgard & Campau), 1963.

" transita (Lipina), 1955.

" triznae (Lebedeva), 1954.

" utahensis (Zeller), 1957.

Genus ENDOSTAFFELLA Rozovskaya, 1961.

Endothyra Moeller, 1880 (pars) (non Brown, 1843)
Girty, 1914.
Lebedeva, 1954 (pars).
Eostaffella Rauser-Chernoussova, 1948 (pars)
Eostaffella (Seminovella) Rauser-Chernoussova, 1951.
Millerella Ganelina, 1956 (non Thompson, 1942).
Durkina, 1959.
Quasiendothyra Rauser-Chernoussova, 1948 (pars).
Ganelina, 1956 (pars).
Orlova, 1958.
Paramillerella E.J. Zeller, 1957 (pars).
Novella Rauser-Chernoussova, 1951 (pars).
Grozdilova & Lebedeva, 1960 (pars).
Endostaffella Rozovskaya, 1961 and 1963 (pars).

Type Species:

Endothyra parva Moeller, 1880, p.26-29,
Plate V, fig.1,a,b.

Description:

Test free, small, discoidal or lenticular, coiled in a plectogyroid spiral with rapidly decreasing axial rotation, approaching planispiral condition in outer whorls, but maintaining partially involute-evolute asymmetrical arrangement of whorl, with from 3-5 whorls,

low chamber counts, 4-6 in first whorl, 6-8 in second, 8-12 in third, 8-14 in fourth, and 9-15 in the fifth whorl; periphery broadly rounded, sweeping smoothly into lateral slopes; chambers inflated, rapidly expanding in size, particularly in final whorl, in axial sections asymmetrically arranged, sub-circular to arched, in sagittal sections quadrate, or rectangular, with width greater than height, very strong peripheral inflation in last half whorl; sutures distinct depressed in final whorls, obscure in early part of the test; septa moderately to strongly anteriorly directed, poorly differentiated from the spiral wall, most particularly in later chambers; protheca thin, dark, undifferentiated, finely granular; secondary deposits very scarce, usually absent, sometimes producing very weak pseudochomata in final whorls; aperture low semi-:circular or lunate slit at base of apertural face and reflecting its asymmetry; proloculum small spherical.

Comparison and Affinities:

Erected in 1961 by Rozovskaya to embrace forms of the group Eostaffella parva Moeller, this genus has been considered as a junior synonym of Endothyra by Loeblich & Tappan (1963), who considered the plectogyroid coiling alone as the diagnostic feature of the two genera. Russian authors (Rozovskaya, 1961, and 1963, Ganelina, 1956) regard the spiral as having two major

planes of coiling; the inner and outer whorls being separated by an abrupt change in coiling of about 90 degrees. This interpretation results from superficial examination of axial sections in which, commonly, the first whorl is at right angles to the final whorl, but more careful examination reveals that intermediate whorls lie in intermediate positions, and there is no evidence to suggest an abrupt change. Moreover, the final whorls cannot be regarded as planispiral for they maintain a distinct asymmetry of form, which demonstrates continuing axial rotation, as has been discussed previously in Endothyra (p.82, Text figs.4,5). The character of the coiling of Endostaffella suggested a similarity to Quasiendothyra and, indeed, a number of its species were formerly refered to that genus (Ganelina, 1956, Orlova, 1958). Quasiendothyra, however, differs in its more complex wall, apertural, and epithecal characters, and its coiling is not directly comparable with that of Endostaffella for in its main development it is irregularly streptospiral, becoming more symmetrical in more advanced forms such as Q. kobeitusana Rauser-Chernoussova but, even then developing an irregular initial stage. On the basis of the coiling Rozovskaya (1961, 1963) assigns Endostaffella to the family Quasiendothyridae but, as has been previously argued

(p.72), it is considered that the highly specialised quasiendothyrids are probably not ancestral to simpler Carboniferous genera.

Endostaffella may be differentiated from Endothyra by its more evolute spiral with axial rotation slowing rapidly in final whorls, smaller size, much thinner wall, more numerous chambers, and particularly, and most significantly, very thin secondary deposits without vestibular ridges.

Endostaffella can be differentiated from Mediocris by its plectogyral coiling, and the lack of heavy axial fillings. It is considered to be closely related, and probably ancestral, to Novella from which it can be differentiated by continuing asymmetry of coiling in all whorls, more rapidly expanding spiral, having fewer and more inflated chambers, especially in the final whorl.

The relationship between Endostaffella and the primitive subgenus Chernousovella, is a close one particularly in species of Chernousovella in which asymmetry of coiling continues beyond the initial whorl. However, the subgenus Chernousovella can be distinguished in axial sections by sub-angular or angularly rounded periphery with chambers finally embracing the early whorls symmetrically, showing that the coiling has become planispiral, and in sagittal

sections by less inflated quadrate chambers which continue uniformly, and do not show the rapid expansion and inflation typical of Endostaffella.

The development of chamber form in Endostaffella in sagittal sections is striking. In the early whorls the chambers appear quadrate, weakly inflated, with septa very often quite strongly differentiated from the spiral wall; a condition which is virtually indistinguishable from sagittal sections of the subgenus Chernousovella, or, indeed, the subgenus Paramillerella. In later whorls, however, the septa become more strongly anteriorly directed, and chambers increasingly inflated until, in the final whorl, they may approach a condition of chamber form typical of Zellerella gen. nov, or even occasionally, in the last one or two chambers, a form approaching that seen in Chernyshinella with very short septa and very strong interseptal inflation. Thus in Endostaffella the ontogeny of chamber form appears to reverse the phylogenetic trend believed to be operative in the development of chamber form in endothyrid foraminifers.

Preservation and Matrix:

The preservation of Endostaffella parallels broadly that to be seen in Endothyra or Paramillerella. No evidence of pores, however, has been noted in its

very slender wall. Although the wall of Endostaffella does show the effects of recrystallisation or replacement a little more rapidly than Endothyra and Paramillerella this is attributed to its slenderness allowing grain growth to disrupt the wall at a stage when it would not be apparent in thicker walled forms. For the most part, Endostaffella maintains fine granular wall despite extensive redistribution in the host sediment.

Horizon and Facies:

Endostaffella has a similar distribution in the Carboniferous of Great Britain and the U.S.S.R., appearing first in Lower Visean, and becoming an abundant and widespread form in Middle and Upper Visean. It continues abundantly into the Namurian but occurs with rapidly diminishing frequency in Middle Carboniferous strata. The genus is recorded from the Mississippian of the United States (Girty, 1914 and Zeller, 1957, Pl.75, fig.1), but it appears to be a comparatively rare form. It has not yet been recorded from the Carboniferous of Japan.

Previously Described Species:

The following species are considered to be referable to this genus:

Endostaffella delicata Rozovskaya, 1963.

Endostaffella elegantula (Rauser-Chernoussova) 1951.

" fucoides Rozovskaya, 1963.

" mira (Rauser-Chernoussova) 1951.

" miranda (Rauser-Chernoussova) 1948 (= Quasiendothyra fucosa Ganelina, 1956; Q. vera Orlova, 1958 parva (Moeller) 1880 = Eostaffella prisca var. butinae Ganelina, 1951: = E. paraparva Ganelina, 1951; = Endothyra barazssiensis Lebedeva, 1954).

" primitiva (Rauser-Chernoussova) 1948.

" pauperis (Durkina) 1959.

" zakharovi (Boghush & Juferev) 1960.

" discoidea (Girty) 1914 (= Eostaffella parva var. shamordini Rauser-Chernoussova, 1948).

ENDOSTAFFELLA MODICA sp. nov.

Plate 11, Figs. 1-14.

Description:

Test free, small, discoidal, umbilicate sometimes asymmetrically coiled in a plectogyroid spiral with decreasing rotation, approaching planispiral condition in final whorls, but asymmetry present throughout spiral, with from 3-4½ whorls, tightly coiled in early part but expanding more rapidly in later whorls, with 5 chambers in first whorl, 7 or 8 chambers in second whorl, 9-10 chambers in third whorl, and 9-13 chambers in fourth whorl, a mean total of 22 chambers at the third whorl, and 32 at the fourth; umbilicus very broad, shallow; periphery broadly rounded sweeping in smooth curve into lateral slopes; chambers moderately inflated in early whorls, strongly inflated in final whorl of complete specimens, in axial sections, semicircular to arched, asymmetrical with one axial prolongation extending beyond the other; chambers, in sagittal sections, quadrate in early whorls, becoming inflated, sometimes with width exceeding height in rapidly expanding chambers of final whorl where periphery is strongly lobulate; sutures distinct depressed in final whorl, obscure in earlier part of tests; septa moderately differentiated from spiral wall in early whorls, becoming shorter,

strongly anteriorly directed in final whorl, often forming smooth sweeping curve with spiral wall; protheca thin (5-8 microns, more rarely up to 10 microns) dark, undifferentiated, finely granular; secondary deposits absent; aperture low slit at base of apertural face reflecting its asymmetry; proloculum small spherical.

Dimensions:

See Tables Nos.5 - 7 below.

Holotype No.P.444/3.

Whorl No.	Prol.	1	2	3	4	4.75
Chambers		5	8	10	10	9
Diameter in Microns.	17	60	94	172	275	353

Depository:

Hunterian Museum of the University of Glasgow, specimen Nos.P.444/1-9 from Index Limestone, Poniel Water, Coalburn, Lanarkshire, and Nos.P.445/1-10 from Lyoncross Limestone, Whitecraigs, Renfrewshire, and Nos.P.446/1-14 from Lyoncross Limestone, Overlee, Clarkston, Renfrewshire.

Comparison and Affinities:

Very little comparative material is available of Endostaffella in sagittal sections, and therefore the following comparisons are subject to the limitations

inherent in the comparison of axial sections. Endostaffella modica is closely similar to E. prava (Moeller) and E. fucoides Rozovskaya, but differs in smaller diameter at corresponding whorls, lower form ration, and more evolute umbilicate test. It is very similar to E. discoidea (Girty) in the umbilicate test, and lack of secondary deposits, but differs in having a smaller test at corresponding whorls, and in having a lower form ratio. E. modica is differentiated from E. inflata sp. nov. by its higher chamber counts and much less inflated chambers.

Horizon and Facies:

In the lowermost limestones of the Upper Limestone Group Endostaffella modica forms one of the dominant components of the assemblage, and is the most abundant species at a number of localities, particularly in association with abundant Girvanella coated bioclasts, and a rich benthonic attached microfauna; Stacheoides, Aoujgalia, Calcivertella, Calcitronella, Orthovertella, etc. E. modica has also been recorded as a rare form in similar facies in the Castlecary Limestone at the top of the Upper Limestone Group, but it has not been observed at intermediate horizons.

Statistics:

The following univariate parameters are recorded:

N = Number of Specimens.

x = Mean.

S = Standard deviation.

ex = Standard error of mean.

V = Coefficient of variation.

OR = Observed Range.

All dimensions are given in microns.

See Tables 5, 6 and 7.

TABLE NO. 5

Population from Index Limestone, Poniel Water.

CHAMBERS

Whorl No.	Prol.	1	2	3	4
N	7	7	7	7	4
x		5	7.29	10.14	10.5
s		0	0.76	0.37	0.55
ex		0	0.29	0.14	0.27
V		0	10	4	3
OR		5	6-8	10-11	10-12

DIAMETER

x	18	55	101	172	267
s	0.7	5	15	19	24
ex	0.3	2.0	5.5	7.1	12.2
V	4	9	15	11	9
OR	17-19	47-60	86-120	146-206	232-292

Spiral Ratio		1.83	1.70	1.55
Whorl Frequency			3	4

FORM RATIO

Whorl No.	1	2	3	4	
Diameter	60	112	189	327	P.444/2
Axial Length	-	69	86	138	P.444/2
Form Ratio	-	0.61	0.45	0.41	P.444/2
Diameter	60	103	172	275	

FORM RATIO

Whorl No.	1	2	3	4	
Diameter	60	112	172	275	P.444/7
Axial Length	-	56	69	95	P.444/7
Form Ratio	-	0.54	0.4	0.34	P.444/7

TABLE NO. 6

Population from Lyoncross Limestone, Whitecraigs

CHAMBERS

Whorl No.	Prol	1	2	3	4
N	6	6	6	6	5
x		5	7.17	9.5	10.4
s		0	0.98	0.55	1.78
ex		0	0.4	0.22	0.78
V		0	14	5	16
OR		5	6-8	9-10	8-13

DIAMETER

x	60	105	183	299
s	5	21	48	44
ex	2.2	8.7	19.7	18.1
V	9	20	26	15
OR	52-69	86-129	120-249	224-335

Spiral Ratio	1.75	1.74	1.63
Whorl Frequency		1	5

FORM RATIO

Whorl No.	1	2	3	4	Outer
N	4	4	4	1	3
x	-	0.675	0.408	0.31	0.397
s	-	0.053	0.069	-	0.006
ex	-	0.026	0.034	-	0.003
V	-	8	16	-	2
OR	-	0.63-0.75	0.35-0.5	0.31	0.34-0.4

TABLE NO. 7

Population from Lyoncross Limestone, Overlee.

CHAMBERS

Whorl No.	Prol.	1	2	3	4
N	9	9	9	9	2
x		5	7.22	9.56	10
s		0	0.67	0.88	2.83
ex		0	0.22	0.29	2.0
V		0	9	9	28
OR		5	6-8	8-11	8-12

DIAMETER

x	20	57	100	168	254
s	4	9	16	24	30.4
ex	1.2	2.8	5.2	8.0	21.5
V	18	16	16	14	12
OR	17-28	43-73	86-129	146-215	232-275

Spiral Ratio	1.75	1.68	1.51
Whorl Frequency		7	2

FORM RATIO

Whorl No.	1	2	3	4
N	5	5	5	4
x	-	0.59	0.438	0.378
s	-	0.154	0.023	0.030
ex	-	0.064	0.010	0.015
V	-	26	5	8
OR		0.46-0.85	0.41-0.47	0.35-0.42

ENDOSTAFFELLA INFLATA sp. nov.

Plate 11, Figs. 15-20.

Description:

Test free, small, discoidal, umbilicate, coiled in a plectogyroid spiral with axial rotation decreasing rapidly from early whorls and not extending much beyond 90 degrees, approaching planispiral condition in final whorls, but asymmetry present throughout spiral, with from 3-4 whorls, expanding rapidly in final whorl, with 5 chambers in the first whorl, 6 or 7 in the second, 7 or 8 in the third, and 8-10 in the fourth, a mean total of 18 chambers in the third whorl, and 26 in the fourth; umbilici very broad, shallow, commonly asymmetrical; periphery broadly rounded sweeping in smooth curve into lateral slopes; chambers inflated in early whorls, very strongly inflated in final whorls, in axial sections, semi-circular to arched, asymmetrical with one axial prolongation extending beyond the other; chambers in sagittal sections quadrate in early portion, but rapidly expanding and culminating in final whorl in a series of highly lobulate chambers chernyshinellid in aspect; sutures strongly depressed giving distinctly lobulate outline in final whorl; septa strongly anteriorly directed throughout the greater part of the test, very short

in final whorl, curving smoothly into spiral wall, but more strongly differentiated in the earlier part of the test; protheca thin (5-8 microns) dark, undifferentiated, finely granular; secondary deposits absent, aperture low slit at base of apertural face reflecting its asymmetry; proloculum small spherical.

Dimensions:

Holotype No.P.448/3.

Whorl No.	Prol.	1	2	3	4	5
P.447/1 -						
Chambers		?	6	8	8	
Diameter	18	60	77	148	232	
P.447/2 -						
Chambers		5	6	7	8	
Diameter	17	34	86	155	258	
P.448/1 -						
Chambers		5	?	8	8	8
Diameter	16	43	-	112	189	292
P.448/2-						
Chambers		?	6	7	10	
Diameter	22	47	95	155	249	
P.448/3 - Holotype.						
Chambers		?	6	7		
Diameter	?	43	95	172		

Whorl No.	Prol.	1	2	3	4	5
P.488/4 -						
Diameter	20	60	77	129	232	
Axial Length		-	43	60	95	
Form ratio		-	0.55	0.46	0.40	
P.499 -						
Chambers		5	6	7	7	
Diameter	18	43	69	103	172	

Depository:

Hunterian Museum of the University of Glasgow, specimens Nos.P.447/1-2 from thin limestone band 2ft. above Calmy Limestone, River Nethan, North of Auchlochan House, Lesmahagow, Lanarkshire: Nos.P.448/1-4 from Orchard Limestone, Poniel Water, Coalburn, Lanarkshire; and No.P.449 from Orchard Limestone, Garpel Water, Muirkirk, Ayrshire.

Comparison and Affinities:

Endostaffella inflata closely resembles E. modica sp. nov. in umbilical character, and peripheral shape, but differs in the much more inflated character of its chambers, resulting in lower chamber counts, and a much more strongly lobulate peripheral outline. Although the number of specimens available for the description of this species is limited, there is sufficient to suggest that the differences in chamber count will be

statistically significant.

Horizon and Facies:

A rare form in argillaceous bioclastic, and often encrinital, limestones and shales of the Orchard position, and thin limestone bands of similar facies overlying the Calmy Limestone.

Genus NOVELLA Grozdilova & Lebedeva, 1950.

Endothyra Brady, 1876(pars) (non Brown, 1843).

Novella Grozdilova & Lebedeva, 1950 and 1960 (pars).

Rauser-Chernoussova et al, 1951.

Miklukho-Maklay, Rauser-Chernoussova, and Rozovskaya, 1959.

Rozovskaya, 1963.

Quasiendothyra Brazhnikova, 1956 (non Rauser-Chernoussova, 1948).

Ganelina, 1956 (pars).

Loeblichia Cummings, 1955.

Voloshinova & Reitlinger, 1959.

Brazhnikova, 1962.

Rozovskaya, 1963.

Nanicella Brazhnikova, 1956 (non Henbest, 1935).

Millerella Zeller, 1950 (pars).

Type Species:

Novella evoluta Grozdilova & Lebedeva, 1950, p.21-22, Plate 1, fig.19.

Description:

Test free, small to medium dimensions, discoid or complanate, strongly compressed axially, planispiral, evolute throughout, or with distinctly asymmetrical coiling in more involute early whorls, with from 3-10 whorls; periphery broadly to moderately rounded,

usually lobulate; chambers small, numerous, inflated, quadrate in sagittal sections; sutures depressed distinct in later portion; septa, anteriorly directed, curved, poorly to moderately differentiated from spiral wall; protheca very thin, dark, finely granular, homogeneous; secondary deposits sparse, usually absent in early whorls, developing thinly and irregularly, or strongly in later whorls; pseudochomata, more rarely chomata; aperture terminal lunate opening at base of apertural face.

Comparison and Affinities:

The present systematic treatment of the genera Loeblichia and Novella appears to be contradictory for, although the genera are morphologically identical, completely contrasting phylogenetic and familial relationships have been postulated for these forms. Although examples of isomorphism are common in foraminifers, in this case, differentiation of these genera appears to result from the emphasis placed by Cummings (1955) on the altered condition of the wall of Loeblichia: a condition which was supposed to be in contrast to the preservation of contemporary endothyrid genera, Endothyra, Paramillerella, etc.. This theme was followed by Fomina, (1958), and has been accepted by other workers, notably Voloshinova & Reitlinger (1959)

Rozovskaya (1963), Loeblich & Tappan (1964). A large number of specimens have been examined from the Upper Limestone Group, and it has been clearly established that the alteration of the wall is quite concomittant with that observed in Endothyra, Endostaffella, and Paramillerella, and is certainly not comparable with with the sensitivity to alteration displayed by staffellid species such as Pseudoendothyra diaphana sp. nov. The wall of Loeblichia is extremely thin and slender, and consequently the effects of recrystallis-:ation become more rapidly apparent. Moreover, because of the slender wall, it is more translucent, even when well preserved, than the thicker walls of larger endothyrids. Cummings' conclusions are based largely on the study of Brady's type material which, as Cummings himself (1955A, p.223) points out, because of the methods of collection, probably contains a disproportionate amount of weathered and altered material. The observations of Fomina (1958 p.122) were based on the species Quasiendothyra miranda Rauser-Chernoussova a form whose correct generic placing appears to lie with the genus Endostaffella since it is not planispirally coiled in its later whorls. Furthermore, a synonym of this species, Q. vera Orlova has been described displaying a normal dark wall, and there is no doubt that species such as Q. ukrainica Brazhnikova and

Q. fucosa Ganelina, although assigned to Loeblichia, do not differ substantially from Novella in wall structure. The only possible character on which Loeblichia and Novella might be differentiated is the character of the secondary deposits and, while Cummings recorded a complete absence of chomata in Loeblichia ammonoides, it is established that secondary material occurs as pseudochomata in outer whorls of species such as L. ukrainica Brazhnikova, or L. adducta Ganelina. The development of more massive chomata in Novella simply follows the trend for increasingly heavy secondary deposits already established in Paramillerella and Endothyra. Similarly, the comparatively planispiral development and large size of Novella follow trends here established in Paramillerella and common to phylogenetic development of endothyrid genera as a whole.

It is, therefore, considered more correct to consider the genus Loeblichia as a junior synonym of Novella. The phylogenetic development of Novella from the more primitive Loeblichia is much more feasible morphologically than its development from Millerella through species such as Millerella elegantula Rauser-Chernoussova whose affinities are clearly with Endostaffella, and not the involute and later uncoiling Millerella. Furthermore, in the latter interpretation,

the genera are essentially contemporaneous and, however attractive such a phylogeny may seem, it is unlikely without extremely rapid and marked morphological changes which are not characteristic of established endothyrid phylogenies.

In the strong asymmetry of its early whorls in primitive species Novella closely resembles Endostaffella, and, indeed, may be derived from this genus through species such as Endostaffella miranda (Rauser-Chernoussova) which has characters common to both genera; its chamber form resembling Novella, but the coiling demonstrating its relationship to Endostaffella. Novella can be differentiated from Endostaffella by its more closely coiled and more numerous planispiral whorls with a large number of small chambers.

The development of Loeblichia from a quasiendothyrid ancestor as envisaged by Reitlinger (1958), Voloshinova & Reitlinger (1959), and Rozovskaya (1963), is suggested largely by the wall structure, and to some extent the mode of coiling. But, as has been considered in the systematic discussion, the quasiendothyrids are a group of advanced and specialised forms, and simplification of their biocharacters would reverse the phylogenetic trend towards increasing size and complexity observed in most Upper Palaeozoic

foraminifers. The genera Paramillerella, Endostaffella, Novella and Zellerella, are regarded as having had a common ancestry in a tournayellid-like form, with species such as Zellerella disca (Zeller) very closely approximating the ancestral type.

Preservation and Matrix:

As has been discussed, the wall of this genus is considered by some authors to be sensitive to recrystallisation, but this results simply from its extreme slenderness. Any grain growth in the wall becomes immediately obvious, whereas in thick walled forms new crystals of the same size remain obscured in the more predominant finely granular matrix. Most of the material from the Upper Limestone Group shows typical homogeneous finely granular dark wall (Plate 12, fig.5). From strongly dolomitised horizons a number of partly recrystallised forms were found (Plate 12, fig.4), including a specimen showing the type of preservation described by Cummings (1955 p.4). However, it is emphasised that the condition of the wall of Novella, given a slight allowance for its dimensions, is completely comparable with that seen in adjacent endothyrid genera.

Horizon and Facies:

Novella is recorded throughout the larger part of

the Carboniferous in U.S.S.R. from Stalinogor zone of lowermost Visean to Kashir zone of Moscovian, Upper Carboniferous. It is, however, known only from Upper Visean and Namurian strata in Great Britain where it is locally abundant in argillaceous limestone and calcareous shale facies. Two sagittal sections recorded by Zeller (1950, Plate 5, fig.14-15) as Millerella sp. suggest the occurrence of this genus in Upper Missippian (Chesteran) strata of U.S.A.

Previously Described Species:

The following species are here refered to the genus Novella.

Novella adducta (Ganelina), 1956.
" ammonoides (Brady), 1873.
" arta (Lebedeva), 1954.
" dainae (Chernysheva), 1940.
" evoluta Grozdilova & Lebedeva, 1954.
" intermedia Rauser-Chernoussova, 1951.
" manukalovae Potievskaya, 1958.
" minima (Brazhnikova), 1952.
" paraammonoides (Brazhnikova), 1956.
" ukrainica (Brazhnikova), 1956.
" urbana (Malakhova), 1954.

NOVELLA MINUTA sp. nov.

Plate 11, Figs.21-24, Plate 12, Figs.1-9.

Description:

Test free, small, laterally compressed, complanate, coiling planispiral in outer whorls, first 1 to 1½ whorls showing distinct axial rotation, typically with 4-5½ whorls, increasing very slowly in height, not embracing more than ¼ of previous whorl, typically with 6 or 7 chambers in first whorl, 9-10 in the second, 10-12 in the third, 12-13 in the fourth, and 13-15 in the fifth whorl, a mean total of 39 chambers in four whorls or 54 in five whorls; periphery broadly rounded in most whorls, sometimes very slightly angular in outer whorls; umbilicus very broad and shallow; chambers slightly inflated, subcircular to arched in axial section, quadrate in sagittal section, sometimes becoming rectangular in last whorl of large specimens, but with width greater than height; sutures distinct depressed in outer part giving lobulate outline, thin and indistinct in earlier whorls; septa, anteriorly directed, slightly curved, not strongly differentiated from spiral wall; protheca very slender (3.5 - 6.5 microns) dark, fine grained, homogeneous; secondary deposits indistinct, possibly very thin basal layer in outer whorls of large specimens, aperture probably

low slit at base of apertural face of terminal chamber; proloculum spherical, small (15-20 microns).

Dimensions:

See Tables 8-10 below.

Holotype P.440/4.

Whorl No.	Prol.	1	2	3	4	5	5.25
Chambers.		?	9	11	13	15	15
Diameter.	20	60	95	138	189	275	167
Width.		-	-	-	-	-	52

Depository:

Hunterian Museum of the University of Glasgow, specimens Nos.P.440/1-5 from Orchard shales, River Avon, Strutherhill, Larkhall, Lanarkshire; Nos.P.441/1-4 from Orchard Limestone, Poniel Water, Coalburn, Lanarkshire; and Nos.P.442/1-3 from thin limestone ribs, 2 ft. above Calmy Limestone, River Nethan, North of Auchlochan House, Lesmahagow, Lanarkshire.

Comparison and Affinities:

This species differs from Novella ammonoides (Brady) in its smaller diameter at corresponding whorls, and in typically developing considerably fewer whorls. It is closely similar to N. ukrainica (Brazhnikova) in form ratio, and number of whorls, but differs in having smaller diameter at given whorls, and in lacking

pseudochomata or, indeed, any distinct evidence of secondary deposits. N. minuta so far as can be determined, can be differentiated from most other species of the genus by its smaller diameter at corresponding whorls, low form ratio, and lack of distinct secondary deposits, but no comparison of chamber counts has been possible. Furthermore, it is considered that in this genus comparison of axial sections is likely to be highly inaccurate because of the difficulty of identifying the first whorl, and ensuring that the section is correctly axial.

Horizon and Facies:

This species is very abundant at certain positions within the Upper Limestone Group, but tends to have a rather spasmodic occurrence. It is a common and abundant form in the argillaceous bioclastic limestones and calcareous shales of the Orchard position, and occurs sporadically in the finely bioclastic argillaceous micrite of the Calmy and Castlecary Limestones but, in some thin argillaceous encrinital bioclastic limestones and shales above the Calmy, it is extremely abundant and characteristic along with Cepekia centrifuga (Brady) and Gen. et sp. nov. Cummings (1961 p.117). Novella has not yet been recorded from the Index and Lyoncross Limestones, where Endostaffella modica sp. nov. is particularly abundant but, in the higher

horizons where Novella minuta occurs abundantly Endostaffella is quite rare.

Statistics:

The following univariate parameters are recorded.

N = Number of specimens.

x = Mean,

S = Standard deviation.

ex = Standard error of mean.

V = Coefficient of variation.

OR = Observed range.

All dimensions are recorded in microns.

TABLE NO. 8

Population from Orchard Shale, Strutherhill

C H A M B E R S

Whorl No.	Prol.	1	2	3	4	5
N	5	4	5	5	5	4
x		6.5	9.4	11.4	13.4	14.5
s		0.58	0.55	0.55	0.55	0.58
ex		0.29	0.23	0.23	0.23	0.29
V		9	6	5	4	4
OR		6-7	9-10	11-12	13-14	14-15

D I A M E T E R

x	18	46	70	103	146	215	microns
s	2	5	14	20	25	42	
ex	1.1	2.5	6.3	9.0	11	20.8	
V	13	11	20	19	17	18	
OR	15-22	43-60	60-95	86-138	129-189	181-275	

Spiral Ratio		1.52	1.47	1.41	1.47
Whorl Frequency				1	4

TABLE NO. 9

Population from Orchard Limestone, Poniel Water.

C H A M B E R S

Whorl No.	Prol.	1	2	3	4	5
N	4	4	4	3	3	1
x		7.25	9	10.67	12	13
s		0.5	0.82	0.58	1	-
ex		0.25	0.41	0.33	0.56	-
V		3	9	5	8	-
OR		7-8	8-10	10-11	11-13	13

D I A M E T E R

x	21	48	80	100	155	206
s	5	3	6	18	23	-
ex	2.6	1.5	2.9	10.3	13.2	-
V	25	5	7	18	15	-
OR	17-28	39-69	56-120	86-120	129-172	206

Spiral Ratio	1.66	1.25	1.55	1.33
Whorl Frequency	1	-	2	1

TABLE NO. 10

Population from thin limestone bands over Calmy Limestone, River Nethan, North of Auchlochan House.

C H A M B E R S

Whorl No.	Prol.	1	2	3	4	5
N	6	6	6	6	5	-
x		6.67	9.33	11.33	12	-
s		0.52	0.52	1.21	1.41	-
ex		0.21	0.21	0.49	0.63	-
V		8	6	11	12	
OR		6-7	9-10	10-13	11-14	

D I A M E T E R

x	18	45	76	115	179
s	2	10	8.5	14.1	27.2
ex	0.6	4.3	3.4	5.7	7.9
V	9	23	11	12	10
OR	16-21	34-60	69-86	103-138	155-206

Spiral Ratio		1.69	1.51	1.55
Whorl Frequency			1	5 -

Data regarding form ratio are lacking, and results are available for only two specimens as follows:-

Whorl No.	1	2	3	4	4½	
Diameter	43	77	120	189	232	P.442
Axial Length	?	30	39	60	60	
Form Ratio	-	0.39	0.32	0.3	0.25	
Diameter	39	69	103	155	181	P.443
Axial Length	?	22	26	39	47	
Form Ratio	-	0.31	0.25	0.25	0.26	

Subfamily OZAWAINELLINAE Thompson & Foster, 1937.

Test discoidal to subspherical, axial length less than diameter, predominantly planispiral, sometimes with axial rotation of the initial whorl, or occasionally later whorls, sometimes with uncoiled stage, typically involute; number of whorls usually less than six; chambers characteristically uninflated, quadrate in early whorls, rectangular in adult whorls; peripheral margin typically angular, keeled to narrowly rounded, more rarely broadly rounded; septa plane, straight or slightly convex, radially directed, meeting spiral wall in sharp angle approaching 90 degrees; protheca finely granular, with extremely fine pores, or sub-alveolar structure, epitheca typically forming thick basal layer and prominent chomata, or pseudochomata; aperture simple terminal basal slit.

Discussion:

The genera Leella, Toriyamaia and Rauserella are transferred to the subfamily Schubertellinae on the basis of their fusiform shape, and probable lack of an aperture. Their inclusion within the Ozawainellinae is founded largely on the discoidal nature of the early whorls although coiling of similar character has been overlooked in Dunbarula and other genera of Schubertellinae.

Genus PARAMILLERELLA Thompson, 1951.

Involutina Brady, 1870 (pars).

Endothyra Brady, 1876 (pars).

Chernysheva, 1948: Lipina, 1955 (pars).

Voloshinova & Reitlinger, 1959 in Rauser-Chernoussova & Fursenko (pars).

Fusulinella (pars) of authors prior to 1952.

Staffella (pars) of authors.

Staffella (Eostaffella) Rauser-Chernoussova 1948G.

Orobias (pars) of authors (non d'Eichwald, 1860).

Millerella Thompson, 1944 (pars), 1945 (pars), and 1948 (pars).

Cooper, 1947 (pars).

Kireeva, 1951: Ganelina, 1951 (pars).

D.N. Zeller, 1953: Malakhova, 1956:

Igo, 1957 (pars): Easton, 1962.

Eostaffella Rauser-Chernoussova, 1948E (nom. nud.)

Vissarionova, 1948: Kireeva, 1949, & 1951:

Rauser-Chernoussova et al, 1951:

Brazhnikova & Potievskaya, 1950 & 1951:

Manukalova, 1950: Ganelina, 1951 & 1956:

Grozdilova & Lebedeva, 1950, 1954 & 1960.

Brazhnikova, 1956: Malakhova, 1956 & 1957:

Putrya, 1956: Golubstov, 1957:

Orlova, 1958: Potievskaya, 1958:

Sheng, 1958: Durkina, 1959:

Eostaffella (continued)

Rauser-Chernoussova, Miklukho-Maklay, and Rozovskaya, 1959, in Rauser-Chernoussova & Fursenko.

Rozovskaya, 1963.

Paramillerella Thompson, 1951.

Thompson, 1954 & 1964.

Petri, 1956: Igo, 1957.

Anisgard & Campau, 1963 (pars).

Osawainella St. Jean, 1957.

Endostaffella Rozovskaya, 1963 (pars).

Type Species:

Millerella advena Thompson, 1944, p.427-429, Plate 1, figs.10-14.

Description:

Test free, discoidal to subspherical, very slightly evolute to involute, planispiral except for the initial whorl, which may show marked axial rotation sometimes leading to slight asymmetry of later coiling, polar ends umbilicate to slightly rounded or angular, with 5-8 chambers in the first whorl, 7-14 in the second, 9-18 in the third, 10-22 in the fourth, and 14-26 in the fifth: chambers moderately inflated to uninflated, in saggital sections quadrate to rectangular, width approximately equal to height in primitive forms,

width less than height in all but the earliest stages of more advanced forms; septa unfluted, straight or curved, slightly to sharply differentiated from the spiral wall; protheca thin, dark, undifferentiated, sometimes reported with a tectum; secondary deposits poorly to very prominently developed, pseudochomate or chomata; aperture low semi-circular or lunate slit at base of final chamber in most species; proloculum spherical to subspherical, small to large, possibly dimorphic.

Ontogeny and Morphogeny:

In populations of primitive species of Paramillerella the majority of individuals show pronounced axial rotation in the first whorl, and, sometimes, the rotation of the whorl is sufficient to produce slight but decided asymmetry in later coiling, as can be seen in Paramillerella versabilis (Orlova). In populations of more advanced species, such as P. hemisphaerica sp. nov., the axial rotation is very slight or absent, but, in others, such as P. radiata (Brady), there is considerable variation from forms with coiling essentially planispiral to individuals with the first whorl initially at right angles to the later coiling.

In a population of 200 specimens of Paramillerella

radiata (Brady) from the Orchard Shale in the Upper Limestone Group, 24 or 12% of the specimens had a very strong asymmetry (approaching 90 degrees) of the first whorl, and in 23 cases out of the 24, the diameter of the proloculum was in the range from 22-26 microns, as opposed to an average for the population of 28 microns, and a range from 17-52 microns. Of 30 specimens with a diameter greater than 35 microns, none showed a significant deviation in coiling, while in the remaining 70% of the population variation from one extreme to the other was observed and, in general, this was related to the diameter of the proloculum. This kind of relationship suggests dimorphism, but, if this is the underlying cause, it does not express itself in the overall size of the test. Of a group of 50 large specimens selected on the basis of having a diameter greater than 0.4 mm. (population mean 0.38 mm.), seven or 14% showed very strong axial rotation of the first whorl and had diameters ranging from 0.44 to 0.60 mm., compared with 0.44 to 0.67 for the group as a whole. As Thompson (1948, & 1964 p.368), has observed, in most fusulinid populations studied the proloculum diameters do not display a bimodal frequency but appear to grade from one diametric extreme to the other. However, Carter's (1953) study of Operculina complanata (Defrance) subsp. japonica Hanzawa has shown

that without careful and accurate study such a relationship can easily be overlooked. In the present case at least, the population having been studied mainly in reflected light, the measurement of proloculum diameters is comparatively inaccurate, nevertheless, it is clear that the mean of proloculum diameters in tests with axial rotation is much lower than that in tests without significant rotation. As the prolocular diameter depends fundamentally on the reproductive process, and is controlled by the amount of growth of the zygote prior to the secretion of the proloculum in a schizont individual, and the scale of division during schizogony, and to some extent the degree of cytoplasmic envelopment of the nuclei in the gamont individual, it is quite possible that two generations may show relatively convergent ranges of prolocular diameter. (Le Calvez, 1938). It is, therefore, possible that although there is no striking morphological divergence, the populations represent both sexual and asexual phases of reproduction; axial rotation having a role similar to the ornamentation of Operculina complanata japonica.

It is quite misleading to consider, as Cooper (1947) and others have done, that the axial rotation in itself represents a diagnostic biocharacter. Such treatment of populations of Paramillerella leads to

the fallacy that forms, having been grouped on the character of the juvenarium, represent species differing in proloculum diameter and overall dimensions. It is not generally appreciated that the axial rotation of the first whorl is related to the diameter of the proloculum, which in turn, because of constant ratio of volumetric increase in chamber size, predetermines the dimensions of the test at successive whorls.

Very little is known regarding the reproductive cycle of fossil foraminifers, except what can be deduced from the study of living forms, and applied to closely related fossil species and genera. Unfortunately, there are no closely allied living representatives of most Upper Palaeozoic foraminifers, and for the most part their life cycles remain obscure. There is, as has been discussed above, evidence that populations of Paramillerella multiplied in phases of sexual and asexual reproduction and, while, this is not strongly expressed morphologically, there are features which support this view. Indeed, it is possible to suggest that schizogony may have occurred during a period of encystment on the sea floor and to suggest that gamogony occurred in a similar manner with the plastogamy of adult gamonts. A common occurrence throughout the calcareous sediments of the Upper Limestone Group are clusters of up to twenty immature individuals of Paramillerella, each

typically with no more than $2\frac{1}{2}$ whorls. That the clusters are not simply the result of winnowing and sorting during sedimentation is evident from the fact that the tests are always of a single species, and are free of any other bioclastic debris. Moreover, they show a considerable amount of internal resorption and the tests appear to be linked to each other by prolongations or fusions of the protheca. The heavily recrystallised appearance of the clusters does not appear to be a primary diagenetic feature, but a result of cytoplasmic activity. Since the clusters contain relatively large numbers of individuals, and have been observed in a few cases associated with a single large mature individual, it is assumed that they represent the content of arrested or abortive schizont cysts rather than the alternative possibility, that they represent spent clusters of plastogamous gamonts. It would seem that the schizont individual, having successfully completed schizogony, becomes trapped in the reproductive cyst along with the new gamont generation. Since it is known that in some foraminifers the new gamont generation consumes the residue of cytoplasm together with much of the carbonate of walls and septa in the schizont adult (cf. Myers, 1938), it may be suggested that the young gamonts, having attained the size at which they would

normally become free of the cyst, turn to one another as a source of further nutrition. In this way their tests may become heavily resorbed and linked together as they sought to absorb one another within their own protoplasmic body. On the other hand, it is possible that they represent simply a breakdown of the initial schizogonic division of the protoplasm, resulting in numerous tests fused together and showing a common protoplasmic body in a gross parallel of the multiple embryonic stage seen in polyvalent individuals.

In a single instance two mature individuals were found with the umbilical regions of the test fused together, but with the test heavily resorbed and interconnecting within the area of union. The proloculum of one of the fused tests had a diameter of 43 microns, compared with the mean for the population at that horizon of 36 microns, and a range of 26-52 microns. It might, therefore, be considered to represent a megalospheric gamont individual and, thus, the fused individuals may be regarded as plastogamous adults, the result of a sexual phase of reproduction.

In most of the populations of Paramillerella which have been examined, sporadic individuals display aberrant coiling, which commonly involves an abrupt shift from one plane of coiling to another, as is seen in Plate 8, fig.2. In a few rarer instances the

direction of coiling is completely reversed (Plate 8, fig.1). The stimuli for such abrupt changes in coiling are not apparent in the examples illustrated, but it seems probable that they result from damage to the final chambers of the growing test; repair of the damaged chamber apparently resulting in reorientation of later growth. Damage to earlier chambers of the whorl results simply in a patch. The specimen, Plate 2, fig.5, shows the repair, by three large blister like chambers, of a damaged section of the final whorl in which the spiral wall and part of the septa have been removed from the peripheral part of the test over a span of six chambers.

The changing condition of the biocharacter of chamber form results in a bioseries of fundamental importance in Paramillerella, and, while chamber form appears to remain conservative and evolve slowly during Visean times, rapid changes occur in the Namurian which gives this biocharacter particular importance both taxonomically and stratigraphically. In the simpler species of the genus, chambers show distinct peripheral inflation with curved septa showing only slight differentiation from the spiral wall. In sagittal sections of some specimens the first two or three chambers immediately following the proloculum may be rather elongate with their width exceeding the height,

but this stage is rapidly followed by more quadrate chambers in which the height and width are of similar dimensions. The quadrate slightly inflated chambers, with ratio of width to height about 1, are character-:istic of most Visean species of Paramillerella. In more advanced forms the quadrate chambers occur only in the early whorls and are rapidly replaced by chambers which attain a progressively more rectangular form with the width becoming distinctly less than the height of the chamber. Accompanying the dimensional changes in the chambers are important morphological modifications. The inflation of the chambers becomes negligible, and the septa become straighter, being sharply differentiated from the spiral wall at an angle approaching 90 degrees. In axial sections the chambers of primitive species have a broadly rounded periphery with inflated lateral slopes which sweep smoothly into the umbilicus. More advanced forms tend to develop a more lenticular section with a subangular periphery and much flatter lateral slopes which curve sharply into the umbilicus. However, the variation in form of the chambers in axial sections does not strongly influence the proportions of the chambers in sagittal sections, except in species which become strongly keeled or evolute in the outer whorls, producing long arcuate septa and curved chambers as in Millerella

marblensis Thompson. The trend of the bioseries of chamber form in Paramillerella leads to tests containing progressively larger numbers of chambers as the ratio of chamber width to height decreases, and chamber form becomes wholly subordinated to the demands of overall test architecture.

A further important morphogenetic trend in Paramillerella is the progressive thickening and elaboration of the secondary deposits. Typically in the most primitive species secondary deposits are very thin or absent, and characteristically when they first appear it is as sutural deposits, wedge like thickenings along the base of the septa, running from the septal foramen to the poles of the chambers and sometimes continuing very thinly in the intercameral suture over the peripheral part of the test. Although the sutural deposits may be linked by a thin basal layer, they do not in any significant way modify the peripheral part of the test in the interseptal area as has been demonstrated and discussed by Fomina (1960 p.115). Thus, although sutural deposits on the septal ends may mimic true chomata when cut in a section meeting the septum tangentially, it is incorrect to describe them in this way, for their function appears to be one essentially of reinforcement and strengthening of the test, asopposed to the channeling and directing

of cytoplasmic flow implicit in the levee-like chomata. Secondary deposits become more prominent in the more advanced species of Paramillerella, commonly forming a thick basal layer and true chomata. The appearance of chomata in Paramillerella, while fundamentally related to the progressive thickening of secondary deposits, is quite clearly dependant also on the morphological condition of the biocharacter of chamber form. The interdependence of the biocharacters is demonstrated by the way in which the chambers assume more rectangular form, causing a shortening of the interseptal distance and, thus, promoting the confluence of the progressively thickening sutural wedges in the interseptal zone, leading eventually to the distinctive platform or channel-like modification of the periphery. This relationship is readily demonstrated by comparing the development of chomata in P. ayrensis sp. nov. and P. craigburnensis sp. nov., species which, while showing comparable dimensions at successive whorls and having basal layers of similar thickness, show markedly different septal spacing. In the former species, with wide septal spacing, the chomata rarely develop beyond the platform-like stage (cf. Plate 14, figs,3,4,8,9), while in the latter, with much more closely spaced septa, strongly asymmetrical levee-like chomata produce a distinct channel connecting the septal foramina (Plate 16 fig.1-3).

Comparison and Affinities:

There is some disagreement regarding the validity of the genera Paramillerella and Eostaffella. Russian authors follow Rauser-Chernoussova, Miklukho-Maklay and Rozovskaya (in Rauser-Chernoussova & Fursenko, 1959) and Rozovskaya 1963), in regarding Paramillerella as a subjective synonym of Eostaffella. On the other hand, American authors, such as Anisgard & Campau, would argue that Eostaffella, as a subjective synonym of Millerella, has no validity. In the original diagnosis of Millerella Thompson, 1942, wholly involute forms were not specifically excluded and, indeed, Thompson later (1944 and 1945) included the completely involute species Millerella circuli, M. pressa, and M. advena. Furthermore, Thompson (1948) considered that the genus embraced forms with from slightly to strongly evolute final whorls, although, in practise, a number of species at that time assigned to Millerella showed no evidence of an evolute final whorl (Thompson, 1944 & 1945, and Cooper, 1947).

Eostaffella was first described as a subgenus of Staffella by Rauser-Chernoussova 1948G, although, if the volume numbers are to be relied upon, it received prior publication in Rauser-Chernoussova 1948E, with full generic status, but constituted a nomen nudum, having no formal description or designation of type

species. In the diagnosis of the subgenus Eostaffella no reference was made to the degree of involution of the test, and it is clear that Eostaffella was intended to embrace species all of which could have been appropriately referred to Millerella at that time. It would appear that Rauser-Chernoussova was unaware of Thompson's Millerella, and she certainly gave no indication that Eostaffella should constitute an emendation of Millerella to include only the involute species. It is, therefore, considered that there are grounds for regarding Eostaffella as a junior subjective synonym of Millerella. In comparing the type species, however, the situation is more obscure, for Russian authors (Ganelina, 1951 and Rauser-Chernoussova, Miklukho-Maklay, and Rozovskaya, 1959), interpret Eostaffella parastruvii as a wholly involute form, while Anisgard & Campau (1963), suggest that, as judged by the holotype, it is evolute in the final whorl. In fact, as Thompson suggests in Anisgard & Campau (1963), the figures are too poor to allow proper judgement of their characters, and probably the matter cannot be decided without an examination of type material. It is of interest to note, however, that Rozovskaya (1963) has referred one of Rauser-Chernoussova's (1948G) original species, Staffella (Eostaffella) kasakhstanica to Millerella, which lends

support to the view that Eostaffella should be regarded as a synonym of the latter genus.

Having appreciated the very strongly evolute character of the type species of Millerella, and having found specimens which established the uncoiled nature of this form, Thompson (1951 p.115) emended Millerella to include only strongly evolute and uncoiling species, and erected Paramillerella to encompass the predominantly involute species. If Eostaffella is accepted as a validly proposed genus then it clearly has priority over Paramillerella, but there are characters in the diagnoses in question which may allow some differentiation of the two genera. Thompson (1951) laid particular emphasis on the strongly chomate structure of Paramillerella while Rauser-Chernoussova (1948G) emphasised that in Eostaffella the principal epithecal development was in the form of pseudochomata (i.e. sutural deposits thickening the septa on each side of the aperture). It has been established in the morphological discussion above that the biocharacters of chamber form and epithecal development are interrelated, particularly in regard to the development of chomata and, therefore, subdivision of the genus would depend on the development of true chomata and the more advanced rectangular chamber form. Although the same biocharacters provide the fundamental

basis for the differentiation of genera such as Zellerella gen. nov. and Mediocris, here the bio-characters are independant and suggest differing physiological and phylogenetic origins, while, on the contrary, in Paramillerella a progressive bioseries is established between the morphological extremes of the dependant biocharacters.

In early studies of Eostaffella by Russian authors a broad species grouping was established such as that given by Ganelina (1951 p.179) as follows:

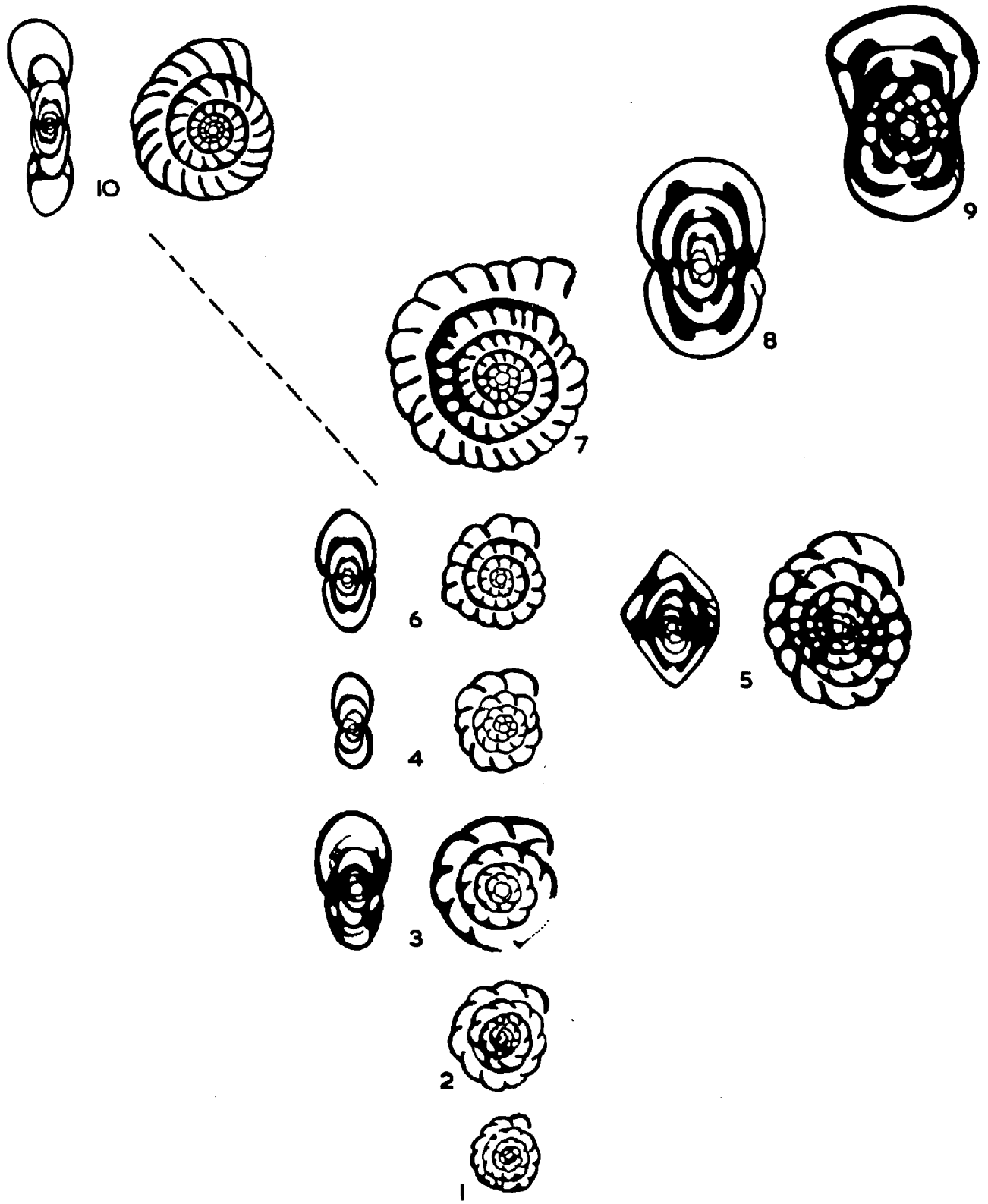
Group, Eostaffella ikensis Vissarionova
Group, Eostaffella mosquensis Vissarionova
Group, Eostaffella parva Moeller
Group, Eostaffella mediocris Vissarionova
Group, Eostaffella protvae Rauser-Chernoussova

In more recent studies Rozovskaya (1961) erected the new genus Endostaffella to embrace, broadly species of the group Eostaffella parva, and this revision is certainly justified for Endostaffella differs from Paramillerella = Eostaffella in having a plectogyroid spiral in which the axial rotation decreases rapidly in the outer whorls, and in having no appreciable epithecal development. Similarly the group Eostaffella mediocris was raised to generic rank by Rozovskaya (1961), and, although Thompson (in Loeblich & Tappan, 1964)

TEXT - FIGURE 6.

An illustration of the development of chamber form in primitive fusulinid foraminifers, showing the relationship of Paramillerella and its new subgenera P. (Chernousovella), P. (Vissarionovella), and P. (Parmillerella) to the related genera Zellerella, Millerella and Pseudostaffella.

1. Tournayella taedia (E.J. Zeller) 1957, primitive sub-tubular chambers.
2. Zellerella disca (E.J. Zeller) 1957.
3. Zellerella symmetrica (E.J. Zeller) 1957, showing elongate chambers with anteriorly directed septa.
4. P. (Chernousovella) chesterensis (Cooper) 1947, showing more quadrate chambers.
5. P. (Vissarionovella) ikensis (Vissarionova) after Rozovskaya 1963, showing inflated angular poles, keeled periphery, and simple quadrate chambers in sagittal section.
6. P.(Paramillerella) indicis sp. nov. with quadrate chambers, well differentiated septa.
7. P. (Paramillerella) craigburnensis sp. nov. showing rectangular chambers.
8. P. (Paramillerella) hemisphaerica sp. nov. showing massive chomata and irregular tunnel path.


10
9
8
7
6
5
4
3
2
1

TEXT - FIGURE 6. - cont.

9. Pseudostaffella needhami Thompson 1942.

10. Millerella marblensis Thompson 1942.

All figures X25 approx.

has placed Mediocris in synonymy with Paramillerella, it quite clearly differs in its pronounced and heavy axial fillings, sub-parallel non-umbilicate axial regions, and more evolute coiling with a broadly rounded periphery and sub-parallel lateral slopes.

The group Eostaffella ikensis differs from typical species of Paramillerella in having a very strongly keeled or sub-angular periphery, flat lateral slopes and inflated convex poles (Text fig.6). The secondary deposits typically form thick pseudochomata, appearing as a long ribbon-like strip running from the aperture to the axial end of the chamber. While the characters outlined define a very distinctive group of species, both morphologically and stratigraphically, they do not appear to reflect any fundamental physiological or phylogenetic contrast with more typical species of Eostaffella. Nevertheless, it is considered that the characters are sufficiently distinctive to warrant the recognition of a new subgenus Paramillerella (Vissarionovella). Similarly, the morphological contrasts of primitive and advanced species of Paramillerella, (Text fig.6), which have been discussed above, and are reflected in the species groups Eostaffella mosquensis and Eostaffella protvae, provide a basis for the recognition of the new subgenera P. (Chernousovella) and P. (Paramillerella).

Preservation of Matrix:

In reviewing the morphology of endothyrid and primitive fusulinid foraminifers the characteristics of wall structure were discussed, and it was emphasised that the protheca represents a uniform structure in which there is a very fine, though normally obscure, transverse system of pores. The evidence for this interpretation is deduced in considerable measure from the characteristics of the wall of populations of various species of Paramillerella within the Upper Limestone Group. Most typically well preserved specimens show no evidence to suggest that the protheca is differentiated, as can be observed in Plate 3, fig.1 and Plates12-15. Furthermore, the distribution of epitheca can be clearly observed, and at no point does it extend uniformly onto the roofs of the chambers to form a lower tectoria. In recrystallised specimens, however, a structure is observed (Plate 3, figs.2 & 3), which can be interpreted in the fashion of Moore (1964 p.297) or Thompson (1942, 1948, 1964, p.396 in Loeblich & Tappan) as a median dark layer, the tectum, with upper and lower tectoria, but the wall is certainly recrystallised as is evident from its relatively inhomogeneous coarsely granular texture, (cf. Plate 3, fig.1 with Plate 3. figs.2-& 3 and Plate 4, fig.2), and, therefore, it is entirely misleading to interpret

its structure in this way. The figures of Millerella marblensis Moore (1964, Plate 47, fig.24 and Plate 48, figs.16 & 17), show an identical texture which suggests that the tectum of primitive fusulinids is of diagenetic origin, representing the interface between the recrystallised epitheca and protheca.

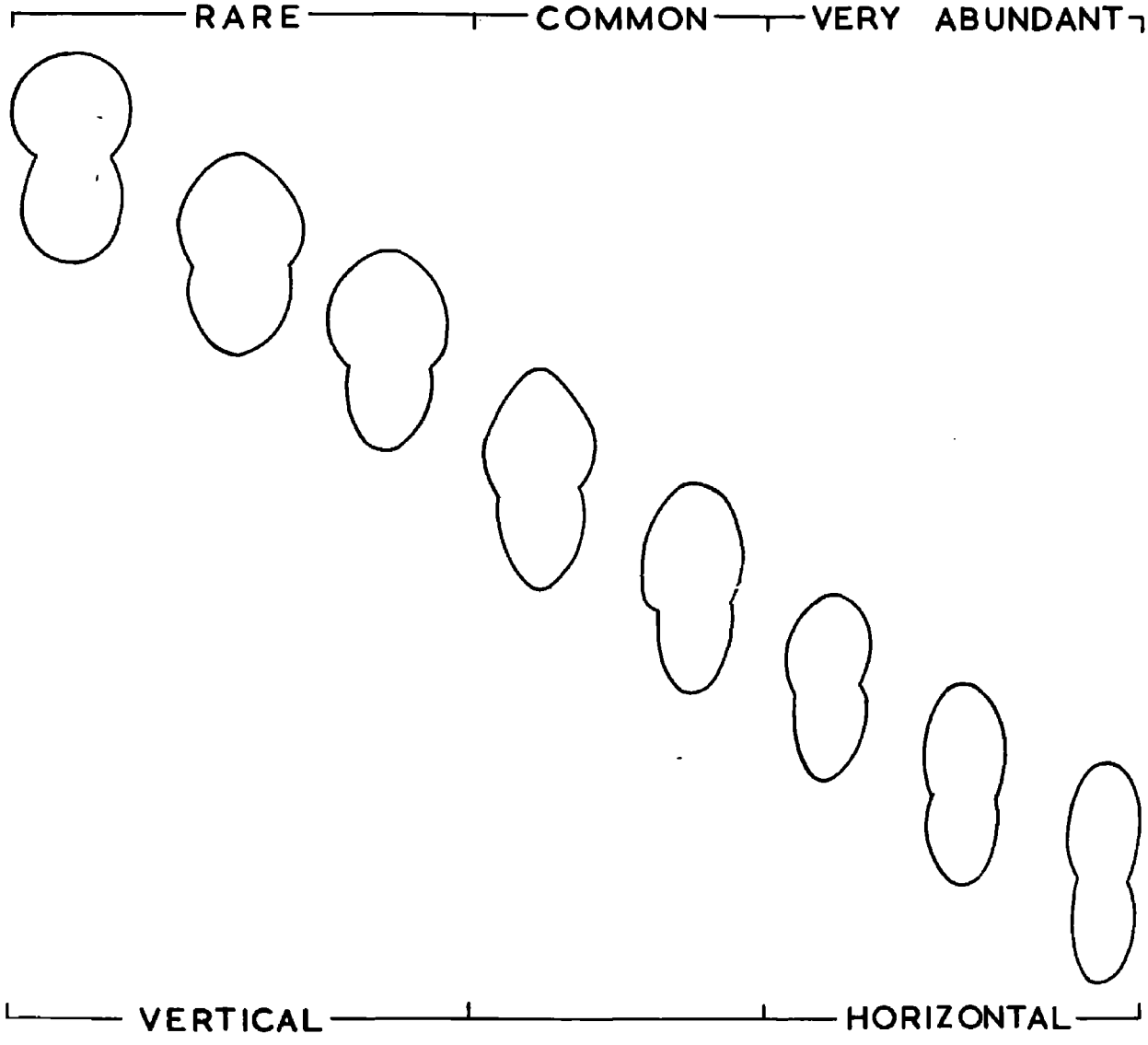
Skinner & Wilde (1954) first demonstrated the presence of pores in Millerella in a specimen in which iron ore infilled the entire test and provided a striking infilling of minute mural pores. A similar, though much poorer, example is figured in Plate 6, fig.3, in which iron enrichment leads to the irregular appearance of transverse structures in the outer whorl, and it is believed that these result from impregnation of some of the pores with iron ore during the heavy staining of the interior of the test. In a single example evidence of an extremely fine alveolar structure has been obtained (Plate 6, fig.1), which implies that the fine structure of the wall of Paramillerella does not fundamentally differ from the keriothecal structure of advanced fusulinids except in the dimensions of the protheca and its pores or alveoli. Undoubtedly the development of alveoli of this size in Paramillerella is exceptional but, nevertheless, the important feature of this specimen is that the alveolar structure can be traced into thinner portions of the wall where, although

it becomes very much more indistinct, provides evidence that it is the fundamental underlying structure of the wall in Paramillerella.

An examination of a population of paramillerellids extracted from shales revealed that while the individuals were all similar in being involute discoidal forms, slightly umbilicate, with 16-20 chambers in the final whorl, three groups could be distinguished on the character of the periphery; those with a moderately rounded periphery; those with a sharp or angularly rounded periphery; and finally those with a broadly rounded periphery. Sectioning failed to reveal any fundamental difference in the internal morphology of the test, and it was, therefore, concluded that the peripheral shape of the tests resulted from compaction. Although in many cases the amount of distortion of the test is marked (Text fig.7), it is not normally accompanied by any noticeable crushing or fragmentation of the test. The last half whorl, in particular, seems particularly prone to distortion even in limestones and appears to have been much more flexible than the rest of the test. The inner whorls show a greater rigidity, and, thus, the peripheral shape of the inner whorls is more constant than that of the outer whorl, but they are more prone to fracture, when distorted, than the outer whorl.

TEXT - FIGURE 7.

Diagram illustrating the variation in peripheral shape in a population of paramiller-:ellids from the shales over the Orchard Limestone, River Avon, Strutherhill. The changes in peripheral shape result largely from distortion of the final whorl during compaction and is consequently dependant on the specimens attitude in relation to the bedding.



Variation in Peripheral Shape
Related to Frequency and Attitude in Relation
to Bedding

It is clear that the disparities in the shape of the periphery of the outer whorls (Text fig.7) result from compaction, the angular forms having come to rest with the plane of coiling parallel to the bedding plane, and the broadly rounded forms with the plane of coiling at right angles to the bedding plane, while the remainder are those which have fortuitously escaped distortion. The forms with the angular periphery are by far the most numerous within the populations studied, as one would expect, since many more specimens come to rest with the plane of coiling parallel or sub-parallel to the bedding than those in a vertical position. Sections of indurated shales indicate that a preferred orientation is much stronger in shales than in limestone, probably because individuals tend to remain in an intermediate position in limestone, while they become rotated towards the plane of the bedding during the compaction of a shale.

Horizon and Facies:

This genus has a world wide distribution, occurring throughout the greater part of the Carboniferous, being absent only from the Tournaisian, but becoming a rare form in the Upper Carboniferous.

In the Carboniferous of the U.S.S.R. the genus, in its more primitive form P. (Chernousovella), appears

first in strata of Lower Visean age, and reaches its greatest variety and abundance in Middle Visean strata where P. (Vissarionovella) becomes abundant and characteristic. The abundance of the species of this genus diminishes gradually in Upper Visean and Middle Carboniferous strata, and P. (Chernousovella) is gradually replaced by P. (Paramillerella), which becomes the dominant form of the Namurian and Middle Carboniferous.

A similar distribution is known in the Carboniferous of Britain and Japan (Igo, 1957), but in the United States the genus does not become important until Upper Chester times, and is of greatest significance in Lower Pennsylvanian atrata.

Paramillerella occurs in all facies which have had a direct link with marine environments. Within the Upper Limestone Group it has been recorded from a range of facies from calcareous sandstones to bituminous, carbonaceous, and phosphatic shales which tends to suggest that it may have been a semi-pelagic form, although from its postulated reproductive encystment it must have been dependant on bottom conditions at least during its reproductive cycle.

VISSARIONOVELLA subgen. nov.

Type Species:

Eostaffella ikensis Vissarionova, 1948, p.219, Plate XIII, figs.8-10, Plate XIV, fig.1.

Description:

Test free, angularly lenticular to rhomboidal, involute, planispiral except for the first whorl, normally shows some axial rotation, polar ends inflated, sub-angular, with 5-6 chambers in the first whorl, 8-9 in the second whorl, 9-14 in the third, 10-16 in the fourth and 13-20 in the fifth; chambers slightly to non-inflated, quadrate in sagittal sections, sometimes slightly rectangular in outer whorls, ratio of chamber width to chamber height about 1 in most stages of growth, in axial sections chambers with angular periphery, flat or very slightly convex lateral slopes with abrupt curve at the polar extremity; septa unfluted, straight or curved, anteriorly directed, moderately to well differentiated from the spiral wall; protheca dark, thin, undifferentiated; secondary deposits moderately developed, basal layer thin or absent, pseudochomata thick ribbon-like, extending uniformly from tunnel to polar ends of the chambers along the septal suture; aperture low slit at base

of final chamber; proloculum spherical small.

Comparison and Affinities:

Vissarionovella is closely related to the new subgenera Paramillerella, and Chernousovella, but is easily distinguished from both these forms by its angular periphery, inflated sub-angular poles, and thick ribbon-like pseudochomata (Text fig.6).

The new subgenus Vissarionovella shows some similarity to Ozawainella but can be differentiated by its greater axial length, less sharply keeled periphery, and the simple, dark, homogeneous character of its protheca.

Horizon and Facies:

This subgenus is characteristic of the Oks substage, Middle Visean of the U.S.S.R., where it first appears in the Aleksin zone, becoming very abundant and character-:istic in the overlying Mikhailov and Venev zones. Vissarionovella does extend, as a much rarer form, into the Serpukov substage, Upper Visean, but is recorded only from the lowermost Tarus zone.

A similar distribution is probable in the Carboniferous of Britain where Endothyra ornata Brady, (1876) is recorded mainly from Middle Visean strata, and is probably referable to the new subgenus Vissarionovella.

Previously Described Species:

The following previously described species are assigned to this subgenus:

P. (Vissarionovella) ikensis Vissarionova, 1948.
Eostaffella ikensis Vissarionova, 1948,
Grozdilova & Lebedeva 1954 and 1960.
Durkina, 1959.
Brazhnikova, 1956.

P. (Vissarionovella) pressa (Durkina)
Eostaffella ikensis var. pressa Durkina, 1959.

P. (Vissarionovella) tenebrosa (Vissarionova), 1948.
Eostaffella ikensis var. tenebrosa Vissarionova, 1948.
Ganelina, 1951.
Grozdilova & Lebedeva, 1954.
Durkina, 1959.

P. (Vissarionovella) proikensis (Rauser-Chernoussova) 1948.

This species was regarded as a synonym of P. (V.) ikensis by Rozovskaya, (1963), who argued that it represented simply juvenile stages of the latter species. This argument was applied to only two of Rauser-Chernoussova's original figures (1948, Plate 16, fig. 22-23). The first of the group of three figures was assigned to a new subspecies, E. ikensis ventricosa on

the grounds that it had a more rapidly expanding spiral. Such a revision is not considered to be justified without more detailed population studies. E. proikensis is a distinctive morphological type which can be distinguished by its smaller size, and less angular polar ends whose inflation forms a narrow umbilicial cavity resulting from the overhang of the last whorl. This species is a form morphologically transitional between the subgenera, Chernousovella and Vissarionovella.

Eostaffella proikensis Rauser-Chernoussova, 1948.
Ganelina, 1951.
Grozdilova & Lebedeva, 1954.
Brazhnikova, 1956.
Durkina, 1959.

Eostaffella proikensis var mstaensis
Ganelina, 1951.

E. ikensis var. ventricosa Rozovskaya, 1963.

The following species on further study may prove to be referable to this subgenus:

Endothyra ornata Brady, 1876.

Eostaffella galinae Ganelina, 1956.

E. raguschensis Ganelina, 1956.

CHERNOUSOVELLA subgen. nov.

Type Species:

Eostaffella mosquensis Vissarionova, 1948, p.222, Plate XIV, figs. 4-6.

Description:

Test free, discoidal, very slightly evolute to involute, planispiral except for the initial whorl, which may show marked axial rotation leading to distinct asymmetry of later coiling, polar ends umbilicate, with 5-6 chambers in the first whorl, 8-9 in the second, 9-14 in the third, 10-16 in the fourth, and 13-18 in the fifth; chambers slightly inflated, quadrate in sagittal sections, sometimes elongate immediately following the proloculum, ratio of chamber width to chamber height about 1, or greater than 1, throughout test; in axial sections chambers with broadly to narrowly rounded periphery, convex lateral slopes curving smoothly or sharply into umbilicus where polar ends of chambers overlap except in the final whorls, which may be slightly evolute in some individuals; septa unfluted, short, curved, poorly to moderately differentiated from the spiral wall; protheca thin, dark, undifferentiated; secondary deposits poorly to moderately developed, basal layer thin or absent, pseudochomata weakly to strongly developed; aperture

low, semi-circular or lunate slit at base of final chamber; proloculum spherical, small.

Comparison and Affinities:

The subgenus Chernousovella differs from P. (Paramillerella) in having fewer, and more inflated, chambers with quadrate axial sections, and in having much thinner secondary deposits which do not modify the periphery of the interior whorls but are confined to sutural thickenings or pseudochomata. (Text figs. 3 and 6).

Chernousovella is distinguished from the subgenus Vissarionovella by its rounded periphery, inflated convex lateral slopes, umbilicate non-inflated or flat axial ends, and in the thinner less conspicuous character of the pseudochomata.

Horizons and Facies:

This subgenus is a widely distributed form and is most characteristic of strata of Visean age. In the U.S.S.R. it appears first in Lower Visean strata, becoming an abundant and dominant form in the Middle Visean, but during the Upper Visean Chernousovella diminishes in frequency, becoming a comparatively rare form in the Middle Carboniferous where it is largely replaced by P. (Paramillerella). A similar distribution is probable in Carboniferous of Britain,

but records of this form are rare in Japan and U.S.A., where it seems to appear for the first time in strata which are probably of Upper Visean age.

Previously Described Species:

The following previously described species are now assigned to this subgenus:

Chernousovella acuta (Grozdilova & Lebedeva), 1950.
" acutiformis (Kireeva), 1951.
" acutissima (Kireeva), 1949.
" asymmetrica (Rozovskaya), 1963.
" aperta (Grozdilova & Lebedeva), 1950.
" amabilis (Grozdilova & Lebedeva), 1954.
" angularis (Brazhnikova), 1956.
" bella (Kireeva), 1951.
" chesterensis (Cooper), 1947 (= Millerella kinkaidensis Cooper, 1947; M. zelleri Cooper, 1947).
Chernousovella chusovensis (Kireeva), 1951.
" cooperi (D. Zeller), 1953.
" constricta (Ganelina), 1951.
" compressa (Brazhnikova & Potievskaya), 1951.
" convexa (Kireeva), 1949.
" decurta (Rauser-Chernoussova), 1948.
" depressa (Putrya), 1956.

Chernousovella designata (D. Zeller), 1953.
" dolixa (Manukalova), 1950.
" donbassica (Kireeva), 1949.
" exilis (Grozdilova & Lebedeva), 1950.
" evoluta (Potievskaya), 1958.
" galinae (Ganelina). 1956.
" graciosa (Manukalova), 1950.
" grandis (Kireeva), 1949.
" gruenwaldi (Malakhova), 1956.
" infirma (Kireeva), 1949
" inflata (Golubstov), 1957.
" infulaeformis (Ganelina), 1951.
" intermedia (Sheng), 1958.
" irenae (Ganelina), 1956.
" kanmerai (Igo), 1957.
" kasakhstanica (Rauser-Chernoussova), 1948.
" kashirica (Rauser-Chernoussova), 1951.
" komatui (Igo), 1957.
" korobcheevi (Rauser-Chernoussova), 1951.
" lenticula (Grozdilova & Lebedeva), 1954.
" lepida (Grozdilova & Lebedeva), 1950.
" lepidaeformis (Kireeva), 1949.
" ljudmilae (Rauser-Chernoussova), 1951.
" minutissima (Rauser-Chernoussova), 1948.
" mixta (Rauser-Chernoussova), 1951.
" mosquensis (Vissarionova), 1948.

Chernousovella mutabilis (Rauser-Chernoussova), 1951.
" nalivkini (Malakhova), 1957.
" oblonga (Ganelina), 1956.
" oldae (Durkina), 1959.
" ovesa (Ganelina), 1956 (= Eostaffella accepta Ganelina, 1956).
" ovoidea (Rauser-Chernoussova), 1948.
" paraprisca (Durkina), 1959.
" parastruvei (Rauser-Chernoussova), 1948.
" pespicabila (Grozdilova & Lebedeva), 1954.
" postmosquensis (Kireeva), 1951.
" pressula (Ganelina), 1956.
" prisca (Rauser-Chernoussova), 1948.
" pseudostruvii (Rauser-Chernoussova & Beljaev), 1936.
" recta (Durkina), 1959.
" rjasanensis (Rauser-Chernoussova), 1951.
" rotunda (Durkina), 1959.
" rossica (Rozovskaya), 1963.
" schwetzovi (Ganelina), 1956.
" settella (Ganelina), 1956.
" singularis (Vissarionova), 1948.
" subsolana (Sheng). 1958.
" subtilis (Durkina), 1959.
" subvasta (Ganelina), 1951.
" transita (Kireeva), 1949.

Chernousovella varvariensis (Brazhnikova & Potievskaya), 1948.

" *vasta* (Rozovskaya), 1963.

" *versabilis* (Orlova), 1958.

" *zelenica* (Durkina), 1959.

PARAMILLERELLA subgen. nov.

Type Species:

Millerella advena Thompson, 1944, pp.427-429, Plate 1, figs. 10-14.

Description:

Test free, discoidal, to subspherical, very slightly evolute to involute, planispiral, except for the initial whorl which may show marked axial rotation resulting in slight asymmetry of later coiling, polar ends umbilicate, with 6-8 chambers in the first whorl, 8-14 in the second, 9-18 in the third, 10-22 in the fourth, and 14-26 in the fifth; chambers with minimum inflation, rectangular in sagittal section, width less than height with ratio less than 1 in all but the earliest stages of growth, in axial sections with narrow sub-angular to very broadly round periphery, flat to strongly convex lateral slopes curving smoothly or sharply into umbilicus where the polar ends of the chambers overlap except in the final whorl of some individuals; septa unfluted, long straight or very slightly curved, sharply differentiated from the spiral wall, protheca thin, dark, undifferentiated, secondary deposits prominently developed, thick basal layer and chomata; aperture low semi-circular or lunate slit at base of final chamber in most species;

proloculum spherical to sub-spherical, small to large.

Comparison and Affinities:

Paramillerella is closely similar to the subgenus Chernousovella, and is clearly closely related, but can be distinguished from that subgenus in the development of chomata, in having rectangular chambers with little or no peripheral inflation, and septa with a sharp angular differentiation from the spiral wall. (Text figs.3 and 6).

The new subgenus Paramillerella can be distinguished from the closely related, and similar, subgenus Vissarionovella by its more rounded periphery, more convex lateral slopes, umbilicate polar ends, distinct chomata, and more rectangular chambers. (Text fig.6).

Horizon and Facies:

The group of primitive fusulinids here refered to the subgenus Paramillerella are exceedingly abundant in the Upper Limestone Group of the Namurian in Scotland. Several species have been described from equivalent horizons in the Carboniferous of the U.S.S.R. and, similarly, the subgenus appears to be most typical of strata of Lower Pennsylvanian age in the United States, and the upper part of the zone of Millerella in Japan.

Previously Described Species:

In this revision the following previously described species are refered to the subgenus Paramillerella:

Paramillerella advena (Thompson), 1944.
" ampla (Thompson), 1944.
" bigemmicula (Igo), 1957.
" chomatifera (Kireeva), 1951.
" circuli (Thompson), 1945.
" derbyi (Petri), 1956.
" inflecta (Thompson), 1945.
" klautzanae (Grozdilova & Lebedeva), 1950.
" n. sp. Easton, 1962.
" pinguis (Thompson), 1944.
" paraprotvae (Rauser-Chernoussova), (= Eostaffella schartimiensis Malakhova, 1956; E. optata Malakhova, 1956).
" postprotvae (Kireeva), 1949.
" protvae (Rauser-Chernoussova), 1948.
" quasiampla (Sheng), 1958.
" radiata (Brady), 1869.
" subsphaerica (Ganelina), 1951.

PARAMILLERELLA (PARAMILLERELLA) INDICIS sp.nov.

Plate 12, Figs.10-20. Plate 13, Figs.1-2.

Description:

Test free, discoidal, involute, planispiral but often with some axial rotation of first whorl, greatest in specimens with smaller prolocula, typically with 3-4 whorls; periphery broadly rounded in earliest whorls, but more narrowly rounded in later whorls; umbilicus broad, shallow or insignificant; chambers in axial sections, with gently convex lateral slopes curving steeply into umbilicus, axial ends overlapping in earlier whorls, sometimes withdrawn in outer whorls; chambers, in sagittal section, weakly inflated, quadrate, lobulate peripherally; septa plane, curved, not sharply differentiated from spiral wall; protheca thin, dark, homogeneous, finely granular; secondary deposits form prominent basal layer and weak platform like chomata; aperture low slit at base of terminal face last chamber; proloculum spherical.

Comparison and Affinities:

This species shows some similarity to P. (Chernousovella) mosquensis Vissarionova, but can be differentiated by its development of chomata, probably higher chamber counts, and lower form ratio. It also

resembles P. (Chernousovella) chesterensis Cooper, but is distinct in its more rapidly expanding spiral, lower form ratio, and most important, the development of chomata. P. (P.) indicis is closely related to P. (P.) radiata Brady, but differs in the quadrate inflated form of the chambers, much thinner secondary deposits, and poorly developed chomata.

The description of this species is based on the study of populations from three localities and two horizons. From the summary of their dimensions given below, it is apparent that the populations from the Lyoncross Limestone differ from those of the Index Limestone.

	Chambers.			
Whorl No.	1	2	3	4
Index, Poniel	5.96	8.89	11.34	13.04
Lyoncross, Overlee	6.09	9.10	11.73	14.67
Lyoncross, Whitecraigs	5.98	8.86	11.6	14.71
	Diameter in Microns.			
Index, Poniel	79	152	267	442
Lyoncross, Overlee	77	145	262	376
Lyoncross, Whitecraigs	76	145	254	381
	Form Ratio.			
Index, Poniel	0.59	0.59	0.56	0.50
Lyoncross, Overlee	0.61	0.62	0.57	0.50
Lyoncross, Whitecraigs	0.61	0.60	0.57	0.51

The differences in the populations are not fully significant statistically but appear to be sufficient to warrant recognition at the subspecific level on the grounds that most of the characters differ at the 95% level of significance. Accordingly two subspecies are recoginsed, P. (P.) indicis indicis, and P. (P.) indicis subradiata, and their full description follows below.

Horizon and Facies:

A characteristic form in the two lowermost horizons of the Upper Limestone Group, the Index and Lyoncross Limestones, P. (P.) indicis enjoys a wide-spread distribution throughout the Midland Valley of Scotland in the Index Limestone, but, as is discussed below, its occurrence is more restricted in the Lyoncross Limestone.

P. (PARAMILLERELLA) INDICIS INDICIS subsp. nov.

Plate 12, Figs.10-17.

Description:

Test free, discoidal, involute, planispiral, but with some axial rotation of the first whorl, greatest in specimens with smaller prolocula, typically with 3-4 whorls, moderately rapidly expanding, ratio decreasing from 1.91 to 1.64, with 6 chambers in the first whorl, 9 in the second, 11 or 12 in the third, and 12-14 in the fourth, a mean total of 39 chambers in four whorls; periphery broadly rounded in earliest whorls, more narrowly rounded in later whorls; umbilicus broad, shallow or insignificant; chambers, in axial sections, with gently convex lateral slopes curving steeply into umbilicus, axial ends overlapping in earlier whorls, sometimes withdrawn in slightly evolute final whorl; in sagittal sections chambers weakly inflated, height approximately equal to width throughout growth, peripheral lobulation distinct; septa plane, convex anteriorly, meeting external wall in broad curve, with slight secondary thickening on posterior surface over the tunnel; protheca thin, dark, homogeneous, finely granular, secondary deposits form basal layer up to twice the thickness of the protheca, absent from roofs of chambers except in

polar extremities; chomata low, forming flat platform like mass on periphery of previous whorl in interseptal area, rising more steeply against apertural face, thinning gradually into poles of chambers, absent in final half whorl; aperture low slit, possibly varying as the tunnel from circular to semi-circular, or lunate opening at base of septum; proloculum spherical.

Dimensions:

See Tables 11 and 12 below.

Holotype P.460/23.

Whorl No.	Prol.	1	1½	2	2½	3	3½
Chambers.		6	8	9	10	10	11
Diam. in Microns	26	86	120	172	224	292	387

Depository:

Hunterian Museum of the University of Glasgow, P.460/1-140 on rock slices 144/1-8, 145/1-6 from Poniel Water, Coalburn, Lanarkshire, Index Limestone, Upper Limestone Group.

Comparison and Affinities:

P. (P.) indicis indicis closely resembles P. (P.) radiata (Brady), but can be differentiated by its significantly lower chamber count, greater diameter, and lower form ratio at successive whorls. Furthermore, it differs in the quadrate inflated form of the chambers,

much thinner secondary deposits, and poorly developed chomata. The main morphological trend observed in the subspecies P. (P.) indicis indicis and P. (P.) indicis subradiata, and the species P. (P.) radiata, are progressive decrease in whorl diameter, and increase in form ratio and chamber count which are associated with changes in chamber form, from slightly inflated quadrate, to non-inflated rectangular, and increase in thickness of secondary deposits and prominence of chomata.

Preservation and Matrix.

Although the limestones in which this subspecies occurs is somewhat recrystallised and dolomitised, the wall remains dark, homogeneous, and fine grained, and is in complete contrast to the preservation of the wall in Pseudoendothyra diaphana sp. nov. in the same limestone.

Horizon and Facies:

This subspecies is confined to the Index Limestone, the lowermost horizon of the Upper Limestone Group, and is an abundant and characteristic form at this horizon where it occurs most abundantly in bioclastic phases of the limestone, but persists in the more argillaceous or sandy portions of the limestone after the disappearance of many other species of the assemblage.

TABLE 11

CHAMBERS

	Prol.	Whorl No. 1	1½	2	2½	3	3½	4
N	75	75	75	73	73	68	56	26
x		5.96	7.71	8.89	10.19	11.34	12.45	13.04
s		0.34	0.58	0.48	0.73	0.85	0.31	1.29
ex		0.04	0.07	0.06	0.93	0.10	0.18	0.25
V		6	8	5	7	8	11	10
OR		5-7	7-10	8-10	9-12	10-14	10-16	11-16

DIAMETER

x	26	79	112	152	202	267	348	442
s	6	8	12	16	21	30	40	57
ex		0.7	0.9	1.4	2.5	3.7	5.4	11.2
V	27	10	10	10	11	11	12	13
OR	17-64	60-95	86-129	112-181	146-249	198-327	258-439	335-542

Spiral Ratio			1.91	1.76	1.72	1.66	1.64
Whorl Frequency		2	-	5	12	30	26

TABLE 12

AXIAL LENGTH

	Prol.	1	1½	2	2½	3	3½	4
		---------- Whorl No. ----------						
N	65	65	65	65	65	63	56	14
x		46	66	90	120	153	188	219
s		5	8	13	16	18	23	24
ex		0.7	1.0	1.6	2.0	2.2	3.0	6.4
V		12	12	10	13	12	12	11
OR		34-60	52-86	69-138	86-155	120-189	138-232	181-258

DIAMETER

x	26	81	113	153	208	277	361	440
s	5	8	12	19	25	33	44	55
ex	0.6	0.9	1.5	2.4	3.2	4.1	5.9	14.6
V	17	10	11	13	12	12	12	12
OR	22-34	69-103	95-146	120-198	163-284	215-378	258-464	344-359

FORM RATIO

x	0.585	0.589	0.587	0.575	0.555	0.531	0.499
s	0.044	0.052	0.050	0.050	0.029	0.054	0.042
ex	0.006	0.007	0.007	0.006	0.004	0.007	0.011
V	8	9	8	9	5	10	8
OR	0.44-0.73	0.47-0.75	0.48-0.65	0.39-0.67	0.49-0.61	0.40-0.73	0.42-0.59

Whorl Frequency	2	7	42	12

P. (PARAMILLERELLA) INDICIS SUBRADIATA subsp. nov.

Plate 12, Figs.18-20, Plate 13, Figs.1 & 2.

Description:

Test free, discoidal, involute, planispiral, but with some axial rotation of the first whorl, greatest in specimens with smaller prolocula, typically with from 3-4 whorls, uniformly expanding, with spiral ratio falling from 1.8 to 1.5 or less, with 6 chambers in the first whorl, 8-10 in the second, 11-13 in the third, and 13-16 in the fourth, a mean total of 41 chambers in four whorls; periphery broadly rounded in earliest whorls, more narrowly rounded in later whorls; umbilicus broad, shallow or insignificant; chambers, in axial sections, with gently convex lateral slopes curving steeply into umbilicus, axial ends overlapping in earlier whorls, sometimes withdrawn in slightly evolute final whorl; in sagittal sections, chambers weakly inflated, height approximately equal to width throughout growth, peripheral lobulation distinct; septa plane, convex anteriorly, meeting external wall in broad curve, with slight secondary thickening on posterior surface over the tunnel; protheca thin, (6-10 microns) dark, homogeneous, finely granular; secondary deposits form basal layer up to twice thickness of protheca, absent from roofs of chambers;

chomata low, forming platform-like mass on periphery of whorl in interseptal area, rising more steeply against apertural face, thinning gradually into poles of chambers, absent in final half whorl; aperture low slit, possibly varying as the tunnel from circular to semi-circular, or lunate opening at base of septum, tunnel path commonly irregular; proloculum spherical.

Dimensions:

See Tables 13-16 below.

Holotype P.462/5.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4
Chambers		6	8	8	10	13	14	15
Diam. in Microns	26	77	103	129	172	215	275	353

Depository:

Hunterian Museum of the University of Glasgow, P.462/1-97 on rock slices 382/1-5, and 381/1 from Lyoncross Limestone, Overlee, Clarkston, Renfrewshire, P.463/1-137 on rock slices 125/2-14 from Lyoncross Limestone, Whitecraigs, Renfrewshire.

Comparison and Affinities:

The subspecies P. (P.) indicis subradiata in its early whorls has chamber counts which do not differ significantly from those of P. (P.) indicis indicis. In whorl three, however, the difference is marginally

significant, and increases to clear statistical significance in the final whorl. A similar relationship can be observed in the diameters of the subspecies, in which differences are marginal at each whorl until the final whorl. The form ratio of P. (P.) i. indicis is probably rather lower than that of P. (P.) i. subradiata, but apart form these differences the two forms show a marked morphological similarity in chamber form and the development of secondary deposits. In contrast, although P. (P.) i. subradiata is similar to P. (P.) radiata in chamber count, diameter, and form ratio, there are distinct morphological differences in the development of chomata, thickness of secondary deposits, and form and inflation of the chambers.

Horizon and Facies:

This species has been recorded so far only from the Lyoncross Limestone, Upper Limestone Group, within the Central Coalfield area of the Midland Valley of Scotland, and it is not recorded from Ayrshire or South Lanarkshire where P. (P.) ayrensis sp. nov. becomes the dominant form. P. (P.) i. subradiata occurs most abundantly in bioclastic limestones in which there is an abundant benthonic encrusting fauna. Most conspicuous are sinuously tangled clots of Girvanella in the matrix and

as thin coatings on much of the bioclastic debris; significantly, such a development of the alga Girvanella is unknown in association with P. (P.) ayrensis.

Statistics:

See Tables 13-16.

TABLE 13

Population from Lyoncross Limestone, Whitecraigs.

C H A M B E R S

	Prol.	1	1½	2	2½	3	3½	4
N	100	98	99	99	99	94	63	28
x		5.98	7.71	8.86	10.38	11.60	13.07	14.71
s		0.35	0.61	0.86	0.68	1.05	1.3	0.9
ex		0.04	0.06	0.09	0.07	0.11	0.16	0.17
V		6	8	8	8	9	10	6
OR		5-7	7-9	8-12	9-14	9-15	10-17	13-16

D I A M E T E R

x	25	76	107	145	194	254	313	381
s	6	13	17	23	33	42	45	46
ex	0.6	1.3	1.8	2.3	3.3	4.3	5.6	8.7
V	22	17	16	16	17	17	14	12
OR	17-43	52-112	77-155	103-224	138-310	181-370	241-456	318-516

Spiral Ratio		1.86	1.81	1.75	1.61	1.5
Whorl Frequency	1	-	5	31	35	28

TABLE 14

Population from Lyoncross Limestone, Whitecraigs

A X I A L L E N G T H

	Prol.	Whorl No. 1	1½	2	2½	3	3½	4	4½
N	37	37	37	37	37	37	35	17	7
x		46	63	86	114	148	180	212	263
s		9	11	16	20	23	27	40	61
ex		1.5	1.8	2.6	3.2	3.7	4.6	9.3	22.8
V		20	18	19	17	15	15	18	23
OR		26-60	43-86	52-120	77-155	95-189	103-232	129-267	146-318

D I A M E T E R

x	26	75	105	144	190	260	336	422	528
s	4	12	18	26	30	45	56	69	87
ex	0.8	2.0	2.9	4.3	5.0	7.5	9.5	16.8	33.8
V	18	17	17	18	16	18	17	16	17
OR	17-34	52-95	69-138	86-215	112-267	155-361	206-439	275-559	370-619

F O R M R A T I O

x	0.614	0.602	0.595	0.592	0.574	0.535	0.505	0.494
s	0.054	0.046	0.039	0.045	.0.048	0.035	0.022	0.048
ex	0.009	0.007	0.006	0.007	0.008	0.006	0.005	0.018
V	9	8	7	8	8	7	4	10
OR	0.50-0.73	0.50-0.71	0.50-0.66	0.48-0.69	0.47-0.73	0.46-0.60	0.47-0.54	0.40-0.54

Whorl Frequency					2	18	10	7

TABLE 15

Population from Lyoncross Limestone, Overlee, Clarkston

C H A M B E R S

	Prol.	1	1½	2	2½	3	3½	4
		---------- Whorl No. ----------						
N	70	70	67	67	66	64	33	12
x		6.09	7.72	9.10	10.65	11.73	13.3	14.67
s		0.29	0.57	0.49	0.73	0.98	1.06	1.21
ex		0.03	0.07	0.06	0.09	0.12	0.18	0.35
V		5	7	5	7	8	8	8
OR		6-7	7-9	8-10	9-12	9-14	11-16	12-16

D I A M E T E R

x	24	77	109	145	197	262	324	376
s	5	8	15	24	28	39	48	43
ex	0.6	1.0	1.8	2.8	3.4	4.9	8.5	12.4
V	20	10	14	16	14	15	15	11
OR	17-43	60-103	86-146	112-206	146-275	181-378	232-413	301-447

Spiral Ratio			1.88	1.8	1.8	1.64	1.43
Whorl Frequency	3	-	1	2	31	21	12

TABLE NO. 16

A X I A L L E N G T H

	Prol.	1	1½	2	2½	3	3½	4
N	25	25	25	25	25	24	18	5
x		44	65	87	114	144	175	218
s		6	10	11	13	18	18	23
ex		1.0	2.0	2.2	2.6	3.7	4.3	11
V		14	15	13	11	12	11	11
OR		34-60-	52-86	69-103	95-138	112-181	146-215	198-258

D I A M E T E R

x	24	73	102	141	192	257	339	442
s	3	8	12	19	25	31	42	59
ex	0.6	1.6	2.5	3.7	4.9	6.4	10.0	26.0
V	14	11	12	13	13	12	12	13
OR	17-30	60-86	77-129	112-181	155-241	206-310	258-413	378-533

F O R M R A T I O

x	0.606	0.630	0.618	0.598	0.565	0.522	0.498
s	0.053	0.058	0.067	0.053	0.044	0.039	0.031
ex	0.011	0.012	0.013	0.011	0.009	0.009	0.014
V	9	9	11	9	8	8	6
OR	0.50-0.73	0.50-0.73	0.53-0.85	0.52-0.78	0.50-0.67	0.45-0.60	0.47-0.55

Whorl Frequency	1	6	13	5

PARAMILLERELLA (PARAMILLERELLA) RADIATA (Brady) 1869.

Plate 13, Figs.3-12.

Involutina radiata Brady, 1869, pp.379-382.

Endothyra radiata Brady, 1873, pp.63 & 95.

Endothyra radiata Brady, 1876, (pars) p.97, Plate V, figs.11a,b. non Plate V, figs. 10 & 12.

Description:

Test free, discoidal, involute, planispiral, but usually with some axial rotation of the first whorl, most acute in specimens with smaller prolocula, insignificant or absent in specimens with large prolocula, typically with from $3\frac{1}{2}$ to $4\frac{1}{2}$ whorls, more rarely 5 whorls, spiral uniformly expanding, ratio decreasing throughout, with 6 chambers in the first whorl, 9 or 10 in the second, 11 to 13 in the third, 13 to 16 in the fourth, a mean total of 42 chambers in four whorls, or approximately 59 in five whorls; periphery broadly rounded in early whorls, becoming slightly more angular in later whorls; umbilicus broad shallow; chambers, in axial sections, with convex lateral slopes curving more sharply into umbilicus, with axial ends overlapping or becoming slightly withdrawn in outer whorls; in sagittal

sections proportions of chambers remain similar throughout, ratio of width to height in early whorls 1, rarely falling below 0.7 in outer whorls, peripheral lobulation very slight; septa plane, straight, anteriorly directed, meeting spiral wall at about 80 degrees, often distinctly thickened by secondary deposits on posterior and anterior surfaces to give a thick stubby or wedge-like outline; protheca thin, dark, finely granular, homogeneous; secondary deposits massive, basal layer commonly up to three times thick-:ness of protheca, sutural deposits occur on anterior faces of septa in wedge-like bodies thinning towards the end of the septa over the tunnel, but not extending onto the roof of the chamber in the interseptal area; chomata massive, asymmetrical distinct throughout test, tapering from tunnel to poles of chambers; aperture low slit, modified in tunnel to a semi-circular, oval, or circular opening; tunnel path often irregular; proloculum spherical, large range in size.

Dimensions:

See Tables 17-20 below.

Lectotype P.35427 (Brady, 1876, Plate V. figs.11a,b)

Diameter: 0.44 mm. Width: 0.15 mm.

Chambers in final whorl: 18.

Paralectotype ex P.35361 (Plate 13, fig.3).

Diameter: 0.35 mm. Width: 0.125 mm.

Chambers in final whorl: 15.

Paralectotype P.31567 ex P.35361.

Diameter: 0.42 mm.

Chambers in final whorl: 15.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4
Chambers		6	8	9	10	12	13	15
Diameter	25	75	98	125	154	210	273	370

Depository:

Lectotype on slide P.35427, and figured Paralectotypes ex slide P.35631, all from Orchard Shale, Gillfoot, Crossford, Lanarkshire, Scotland, in Brady collection of Carboniferous and Permian foraminifers, British Museum (Natural History). Hunterian Museum of the University of Glasgow, P.465/1-55 on rock slices 162/1-4, from Poniel Water, Coalburn, Lanarkshire; P.466/1-53 on rock slices 348/2-10 from Garpel Water, Muirkirk, Ayrshire; and P.464/1-64 on rock slices 26A/1-90, from River Avon, Strutherhill, Larkhall, Lanarkshire.

Comparison and Affinities:

Brady's (1876) original figured types of this species originate from two separate horizons and

localities. The specimen, Plate V, fig.10, from the shales over the Calmy limestone at Gair quarries, Lanarkshire, and Plate V, figs.11a,b, from Orchard shales, Gillfoot, Crossford, Lanarkshire. It has been shown in the present study that populations of species of P. (Paramillerella) from different horizons within the Upper Limestone Group, differ substantially, and, it is, therefore, necessary to define the type more precisely.

The type Plate V, figs.11a,b, is here designated as the lectotype of P. (P.) radiata. Thin sections of syntypes from Brady's collection show that the material from Gillfoot is comparable with samples of populations from Orchard limestone at three other localities. Since the parameters of the three populations do not differ significantly in any character, it is considered justifiable to define P. (P.) radiata from Brady's syntypes and with reference to the populations from the same horizon as the lectotype.

P. (P.) radiata is closely similar to P. (P.) paraprotvae Rauser-Chernousova and further study may show these forms to be synonymous but, in the meantime, adequate comparison is impossible since there is no data available regarding the sagittal sections.

P. (P.) radiata resembles P. (P.) pinguis Thompson, however, its test expands more rapidly in the early

whorls, becomes more closely coiled in later whorls, and has a greater form ratio at corresponding whorls. P. (P.) radiata is closely related to P. (P.) indicis subradiata subsp. nov. and P. (P.) involuta sp. nov., which show very similar characters and dimensions and appear to represent portions of a single lineage or cline segmented by the accident of cyclical sediment-:ation. Although P. (P.) radiata has strong morpho-:logical affinities with P. (P.) involuta in diameter, form ratio, and development of secondary deposits, it differs in a statistically significant manner in chamber count at each whorl, having a mean total of 42 chambers in four whorls, as opposed to 47 in P. (P.) involuta. In contrast P. (P.) radiata differs from P. (P.) indicis subradiata in chambers counts only in a marginally significant way, but it is a more tightly coiled form, differing morphologically in its more rectangular, less inflated chambers, and thick basal deposits with prominent chomata.

Preservation and Matrix:

Observation of material in shale shows that compaction results in considerable modification of peripheral shape and form ratio, particularly in the outer whorls. (see p.170 and Text fig. 7). Some of the material extracted from shales has the chambers

infilled by phosphate (Plate 8, fig.3) in the manner already noted in Plectogyra phrissa (p. 98).

Horizon and Facies:

This species is abundant and characteristic in the Orchard limestone and shales in the Upper Limestone Group, and may extend as a rare form into lower horizons of the Calmy limestons. P. (P.) radiata occurs in greatest numbers in the strongly bioclastic and crinoidal phases of the Orchard limestones.

Statistics:

See Tables 17 to 22.

TABLE 17

Population from Orchard Limestone, Strutherhill.

CHAMBERS

	Whorl No.								
	Prol.	1	1½	2	2½	3	3½	4	4½
N	26	26	26	26	26	23	19	11	5
x		6.15	8.23	9.62	10.69	12.15	13.21	14.45	
s		0.46	0.74	0.68	0.82	0.99	0.98	1.47	
ex		0.09	0.16	0.13	0.16	0.21	0.22	0.44	
V		7	9	7	8	8	7	10	
OR		5-7	7-10	8-11	9-12	10-14	11-16	12-17	14-16

DIAMETER

x	25	72	101	134	178	231	305	374	
s	5	10	15	18	19	27	40	37	
ex	0.9	1.9	2.9	3.6	3.8	5.7	9.3	11.0	
V	19	13	14	14	11	12	13	10	
OR	17-34	60-95	77-129	103-172	138-224	181-301	241-413	301-447	378-593

Spiral Ratio			1.84	1.75	1.73	1.71	1.62
Whorl Frequency				3	4	8	6	3

TABLE NO. 18

A X I A L L E N G T H

	Prol.	Whorl No. 1	1½	2	2½	3	3½	4	4½
N	38	36	37	38	38	36	33	21	7
x		45	64	84	107	134	163	192	235
s		8	12.0	12.1	17	18	23	32	45
ex		1.3	2.0	2.1	2.8	3.2	4.1	7.1	16.8
V		18	19	15	16	14	14	17	19
OR		34-69	43-86	60-112	77-146	103-189	120-224	146-284	181-301

D I A M E T E R

x	26	74	102	137	184	239	315	374	490
s	6	13	17	22	28	35	48	50	75
ex	0.9	2.1	2.8	3.6	4.6	5.9	8.3	11.1	28.4
V	22	15	17	16	15	15	15	13	15
OR	17-103	52-138	77-189	103-267	129-310	172-413	241-507	327-636	413-

F O R M R A T I O

x	0.607	0.626	0.607	0.588	0.559	0.517	0.505	0.477
s	0.059	0.055	0.049	0.051	0.052	0.054	0.045	0.05
ex	0.01	0.011	0.008	0.008	0.009	0.009	0.010	0.019
V	10	10	8	9	9	10	9	10
OR	0.50-0.70	0.50-0.75	0.54-0.75	0.48-0.68	0.45-0.68	0.34-0.61	0.43-0.73	0.42-0.56

Whorl Frequency	2	3	12	14	7

TABLE NO. 19

Population from the Orchard Limestone, Poniel Water

CHAMBERS

	Prol.	1	1½	2	2½	3	3½	4	4½	5
N	43	43	43	43	42	41	29	14	3	2
x		6.14	8.0	9.44	10.84	12.07	13.66	14.5		
s		0.45	0.57	0.58	0.81	0.84	1.27	0.94		
ex		0.07	0.09	0.09	0.13	0.13	0.23	0.25		
V		7	7	6	8	7	9	6		
OR		5-7	7-9	8-10	9-13	10-14	11-16	11-16	13-16	16-17

DIAMETER

x	25	74	105	139	185	239	309	378		
s	6	11	16	22	28	38	51	42		
ex	1.0	1.7	2.5	3.4	4.6	5.9	9.5	11.2		
V	25	15	15	16	16	16	17	11		
OR	17-43	52-103	77-146	103-206	138-267	181-335	224-421	292-439	278-542	473-654

Spiral Ratio		1.89	1.78	1.73	1.66	1.56	
Whorl Frequency		1	1	12	15	11	1	2

TABLE NO. 20

A X I A L L E N G T H

	Prol.	Whorl 1	1½	2	2½	3	3½	4	4½
N	7	7	7	7	7	7	7	6	2
x		42	57	75	106	128	167	195	
s		6	8	13	13	17	26	21	
ex		2.2	3.2	4.9	4.9	6.6	9.5	8.5	
V		14	15	17	12	13	16	11	
OR		34-52	43-69	60-95	77-120	103-155	129-189	163-215	

D I A M E T E R

x	23	70	97	129	177	237	304	391	
s	4	10	8	14	22	27	33	45	
ex	1.5	4.0	6.5	5.7	8.3	10.3	12.0	18.1	
V	18	15	9	12	13	11	11	11	
OR	17-30	60-86	86-112	112-155	146-206	206-284	249-353	318-439	404-525

F O R M R A T I O

x	0.60	0.582	0.564	0.59	0.54	0.579	0.5
s	0.073	0.063	0.049	0.04	0.056	0.064	0.015
ex	0.027	0.024	0.018	0.015	0.021	0.024	0.006
V	12	11	9	7	10	11	3
OR	0.50-0.71	0.50-0.70	0.50-0.65	0.53-0.64	0.45-0.61	0.51-0.69	0.48-0.52

Whorl Frequency 1 4 2

TABLE 21

Population from Orchard Limestone, Garpel Water.

C H A M B E R S

	Prol.	Whorl No. 1	1½	2	2½	3	3½	4	4½
N	42	42	42	42	41	41	33	17	3
X		6.12	8.19	9.38	10.93	12.2	13.58	14.94	
s		0.45	0.63	0.72	0.9	0.92	1.3	1.68	
ex		0.07	0.1	0.11	0.14	0.14	0.80	0.41	
V		7	8	8	8	8	10	11	
OR		5-7	7-9	8-10	9-12	9-14	11-17	12-18	15-17
Whorl Frequency				1	-	8	16	14	12

TABLE 22

A comparison of the mean chamber counts from the localities: Strutherhill, Poniel Water, and Garpel Water.

Whorl No.	1	1½	2	2½	3	3½	4	4½
Struther	6.15	8.23	9.62	10.69	12.13	13.21	14.45	
Poniel	6.14	8.0	9.44	10.83	12.07	13.66	14.5	
Garpel	6.12	8.19	9.38	10.93	12.2	13.58	14.94	

P. (PARAMILLERELLA) INVOLUTA sp.nov.

Plate 13, Figs.13 & 14.

Description:

Test free, discoidal, involute, planispiral, with slight to moderate axial rotation of the first whorl, typically with from $3\frac{1}{2}$ to 5 whorls, rapid increase in diameter at first whorl, thereafter relatively tightly coiled, spiral ratio falling from 1.81 at second whorl to 1.37 at fifth whorl, with 6 or 7 chambers in first whorl, 10 or 11 in the second, 13-15 in the third, 16-18 in the fourth, and 18-21 in the fifth, a mean total of 47 chambers in four whorls, and 67 in five; periphery rounded, of similar contour throughout; umbilicus broad, shallow; chambers in axial sections, with convex lateral slopes curving slightly more steeply into the umbilicus, axial ends overlapping, in sagittal sections proportions of chambers remain similar throughout, ratio of width to height rarely falling below 0.8 in outer whorls, peripheral lobulation slight or absent; septa plane, straight, anteriorly directed, meeting spiral wall at about 80 degrees, often thickened by secondary deposits on posterior and anterior surfaces to give a thick stubby or wedge-like outline; protheca thin, (8-12 microns in final whorls) dark, finely granular,

undifferentiated; secondary deposits massive, basal layer commonly two or three times thickness of protheca, thin sutural deposits occur on anterior face of septa in wedge-like bodies, thinning towards the end of the septa over the tunnel, but not reaching roof of chamber in interseptal area; chomata massive, asymmetrical, distinct throughout test, tapering from tunnel to poles of chambers, aperture low slit, modified in tunnel to a semi-circular or circular opening; tunnel path sometimes irregular, proloculum spherical.

Dimensions:

See Tables 23-24 below.

Holotype P.468/12.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4	4½	5
Chambers		6	8	10	12	14	16	17	17	17
Diameter	26	69	95	129	172	215	267	327	396	516

Depository:

Hunterian Museum of the University of Glasgow, P.468/1-79 on rock slices Nos.225/1-6 from thin limestone band above Calmy Limestone, Upper Limestone Group, Namurian of Spireslack, Glenbuck, near Muirkirk, Ayrshire.

Comparison and Affinities:

This form resembles rather closely Paramillerella pinguis Thompson, however, its test expands more rapidly

in the early whorls, becomes more closely coiled in later whorls, and has a greater form ratio at corresponding whorls. It is very closely similar to P. circuli Thompson, but is more tightly coiled in later whorls, and has a lower chamber count and form ratio. P. involuta shows intermediate characters in the lineage which includes P. craigburnensis and P. radiata (Brady), but it is easily distinguished from these species by its form ratio, chamber count, diameter at successive whorls, whose dimensions lie between those of the other two species.

Preservation and Matrix:

This species, which occurs in a dolomitised, argillaceous, highly crinoidal micrite, commonly has a fragmented and recrystallised final whorl. This would appear to result, in part, from abrasion and crushing during sedimentation in the crinoidal micro-biostromes.

Horizon and Facies.

P. involuta is a distinctive form in the thin argillaceous limestones occurring above the Calmy Limestone at localities in Ayrshire and Lanarkshire.

Statistics:

See Tables 23 and 24.

TABLE 23

C H A M B E R S

	Prol.	1		2		3		4		5
N	54	54	54	54	54	51	41	31	17	7
x		6.46	8.41	10.13	11.93	13.61	15.46	16.90	17.82	19.57
s		0.57	0.75	0.79	1.09	1.24	1.06	1.25	1.81	1.59
ex		0.08	0.10	0.11	0.15	0.17	0.17	0.23	0.44	0.60
V		9	9	8	9	9	7	7	10	8
OR		6-8	7-11	9-12	9-12	11-16	12-18	14-19	14-21	17-22

D I A M E T E R

x	27	81	110	147	192	246	311	378	460	520
s	4	12	13	17	21	28	39	41	57	24
ex	0.6	1.2	1.8	2.3	2.8	3.9	6.0	7.4	13.8	8.7
V	16	11	12	12	11	11	12	11	12	5
OR	22-39	69-103	86-138	120-181	155-232	198-301	249-404	318-456	396-568	499-559

Spiral Ratio	1.81	1.74	1.67	1.61	1.53	1.47	1.37
Whorl Frequency		3	10	10	14	10	7

TABLE 24

A X I A L L E N G T H

Prol.	1		2		3		4		5
N 25	25	25	25	25	25	22	18	13	9
x	45	64	86	111	138	167	209	244	286
s	7	8	10	13	17	23	21	16	17
ex	1.3	1.7	2.0	2.6	3.4	5.0	4.9	4.6	5.6
V	10	11	11	11	11	12	8	9	9
OR	34-60	52-77	69-112	86-138	103-172	129-215	155-249	215-301	241-301

D I A M E T E R

x 27	72	100	136	180	231	293	358	446	543
s 5	7	11	16	20	26	35	30	40	49
ex 1.0	1.4	2.2	3.1	4.1	5.2	7.4	7.0	11.2	15.8
V 19	15	13	12	12	12	14	10	7	6
OR 22-43	60-86	86-120	112-163	138-224	189-301	249-404	310-413	396-525	490-697

F O R M R A T I O

x	0.624	0.638	0.634	0.618	0.59	0.571	0.588	0.555	0.531
s	0.056	0.065	0.071	0.063	0.065	0.060	0.060	0.044	0.059
ex	0.011	0.013	0.014	0.013	0.013	0.013	0.014	0.012	0.020
V	9	10	11	10	11	10	10	13	11
OR	0.44-0.78	0.50-0.80	0.50-0.79	0.48-0.76	0.48-0.63	0.48-0.69	0.45-0.67	0.46-0.61	0.42-0.60

Whorl Frequency					3	4	5	4	9

P. (PARAMILLERELLA) AYRENSIS sp. nov.

Plate 13, Fig.16. Plate 14, Figs.1-11.
Plate 15, Figs.1-6 and Plate 19, Fig.4.

Description:

Test free, discoidal, involute, planispiral, commonly with minor irregularities in the coiling of the first whorl, sometimes with first whorl at high angles to later whorls, characteristically with from $3\frac{1}{2}$ to $4\frac{1}{2}$ whorls loosely coiled, rapidly expanding, particularly in first two whorls, spiral ratio decreasing from 1.9 at second whorl to 1.5 or 1.6 in final whorls, with 6 chambers in first whorl, 9 or 10 in the second, 11 or 12 in the third, and 13 to 15 in the fourth, a mean total of 41 chambers in four whorls; periphery broadly rounded in first whorl, becoming more angular in later whorls, but more broadly rounded in final whorl; umbilicus broad, shallow, sometimes deeper in specimens showing slight evolution of the final whorl; chambers with distinctly convex lateral slopes curving more steeply into umbilicus where axial ends meet or slightly overlap, sometimes showing distinct asymmetry, one end overlapping beyond the other; slight peripheral inflation forming shallow intercameral suture in saggital sections, proportions of chambers similar throughout spire, ratio dropping

from 1 in first whorl to 0.7 or 0.8 in final whorls; septa plane, straight, slender, slightly anteriorly directed, externally recurving posteriorly towards umbilicus, joining spiral wall at an angle of about 70 to 80 degrees, with slightly bulbous ends over the tunnel, due to thickening by secondary deposits, mainly on the posterior surface of the septa; wall thin, dark, homogeneous, protheca with fine pores, thickening at the posterior of each chamber at suture with previous chamber; secondary deposits thick, lighter than protheca, possibly more coarsely granular than protheca, thick basal layer up to twice the thickness of the wall, extending up septa but not reaching roofs of chambers except in polar ends of chambers, chomata present, low, forming flat platform like body on periphery of whorl in interseptal area, becoming massive towards base of the septa, greatly reduced in final whorl; aperture low semi-circular to lunate slit from one quarter to one fifth the height of chamber; proloculum spherical, but often with flat face where pore opens into first chamber.

Dimensions:

See Tables 25-28 below.

Holotype P.472/65.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4
Chambers		6	8	9	9	11	12	13
Diameter	26	86	112	163	224	301	404	542

Depository:

Hunterian Museum of the University of Glasgow, P.472/1-116 on rock slices Nos.194/1-13 from Craigburn, Uddington, Nr. Douglas Lanarkshire, and P.473/1-70 on rock slices Nos.358/1-8 and 359/1, and 9, from Garpel Water, Muirkirk, Ayrshire, all from Lyoncross Limestone, Upper Limestone Group, Namurian of Scotland.

Comparison and Affinities:

This is a distinctive species particularly characterised by the rapid expansion of its spiral in the first two whorls, and by the relatively small number of chambers in whorls of large diameter. It is unlike any of the other species from the Upper Limestone Group. It bears some resemblence to Chernousovella vasta Rozovskaya and Chernousovella oblonga Ganelina but can easily be differentiated from these forms by its greater form ratio, more rounded periphery, thicker secondary deposits with chomata, more rapidly expanding spiral with a greater diameter at any given whorl. The species Chernousovella kanmerai Igo is also similar, but its lower form ratio, much slower expansion in early whorls, and much thinner secondary deposits distinguish it from

Paramillerella ayrensis.

Preservation and Matrix:

Although the host sediment is often weakly to moderately, or sometimes strongly, recrystallised, this species is typically well preserved. The distribution of the lighter secondary deposits can easily be determined against the thin, dark, uniform undifferentiated protheca. Certain specimens show fine, dark and bright lines cutting transversely across the wall, and some of the more striking examples of these transverse structures are illustrated in Plate 6, figs.1 and 2.

Horizon and Facies:

Recorded so far only from the Lyoncross Limestone, Upper Limestone Group, of Ayrshire and certain parts of south Lanarkshire. Although it is a characteristic and abundant form within the area stated, it has not been recorded from the Lyoncross Limestone within the Central Coalfield or the eastern outcrops of the Midland Valley. It occurs in argillaceous facies ranging from argillaceous bioclastic micrites to calcareous poorly bioclastic siltsones and sandstones which are often abundant at, and characteristic of, this particular horizon.

TABLE 25

Population from Lyoncross Craigburn.

CHAMBERS

	Prol	1		2		3		4	
N	81	81	81	81	79	75	57	26	8
x		6.17	7.88	9.36	10.52	11.61	13.05	13.85	14.38
s		0.49	0.76	0.76	0.73	1.11	1.46	1.41	1.5
ex		0.06	0.09	0.08	o.08	0.13	0.19	0.28	0.53
V		8	10	8	7	10	11	10	10
OR		5-8	7-11	8-12	9-14	9-15	11-17	11-17	12-16

DIAMETER

x	31	94	131	181	243	320	414	489	627
s	7	14	22	28	42	53	68	52	68
ex	0.8	1.6	2.4	3.2	3.8	6.1	9.1	10.3	23.9
V	22	15	17	16	17	17	16	11	11
OR	17-52	69-138	86-198	120-267	163-353	215-456	275-602	370-576	507-731

Spiral Ratio	1.91	1.81	1.76	1.71	1.54	1.5
Whorl Frequency	2	4	18	31	18	6

TABLE 26

A X I A L L E N G T H

Prol.		1		2		3		4
N	36	36	36	36	36	34	29	19
x		55	77	100	135	177	213	260
s		8	12	15	18	24	24	32
ex		1.3	2.0	2.6	2.9	4.2	4.5	7.3
V		14	15	15	13	14	11	12
OH		43-69	52-103	77-138	95-181	129-232	172-258	206-318

D I A M E T E R

x	34	89	126	174	236	312	405	510
s	6	10	18	24	34	46	57	74
ex	1.1	1.7	2.9	4.0	5.7	7.9	10.6	16.9
V	19	11	14	14	14	15	14	14
OR	26-	69-120	86-155	120-215	172-301	241-413	310-542	396-662

F O R M R A T I O

x	0.623	0.611	0.573	0.571	0.566	0.531	0.516
s	0.055	0.055	0.037	0.048	0.042	0.046	0.052
ex	0.009	0.009	0.006	0.008	0.007	0.009	0.012
V	9	9	7	8	8	9	10
OR	0.55-0.78	0.50-0.82	0.50-0.65	0.50-0.74	0.50-0.67	0.46-0.68	0.44-0.65

Whorl Frequency	2	5	10	16	

TABLE 27

Population from Lyoncross Limestone, Garpel Water, Muirkirk.

	Prol.	1		2		3		4	
CHAMBERS									
N	50	50	50	49	48	41	38	29	8
X		6.06	7.86	9.35	10.58	11.71	13.05	14.24	15.0
s		0.21	0.57	0.59	0.79	1.02	1.28	1.45	0.5
ex		0.03	0.08	0.08	0.11	0.16	0.21	0.27	0.18
V		3	7	6	8	9	10	10	3
OR		6-7	7-9	8-11	9-13	10-15	10.15	11.17	14-16
DIAMETER									
x	32	94	133	183	247	325	421	523	560
s	5	11	16	23	34	47	63	76	71
ex	0.8	1.6	2.2	3.3	4.9	7.4	10.2	14.1	25.0
V	17	12	12	13	14	15	15	15	12
OR	22-43	77-129	95-181	129-232	172-310	224-378	301-568	396-645	516-705
Spiral Ratio				1.91	1.80	1.80	1.69	1.60	1.42
Whorl Frequency			1	1	7	3	9	21	8

TABLE 28

A X I A L L E N G T H

	Prol.	1		2		3		4	
N	21	21	21	21	20	20	18	10	6
x		53	73	98	126	166	211	255	290
s		8	12	14	20	21	23	34	23
ex		1.8	2.6	3.0	4.5	4.7	5.4	10.8	9.5
V		15	16	14	16	13	11	13	8
OR		34-69.	52-95	77-120	86-155	129-206	172-258	206-318	258-327

D I A M E T E R

x	33	88	122	170	228	306	407	506	629
s	7	13	18	25	33	46	53	51	81
ex	1.6	2.8	3.9	5.5	7.4	9.5	12.9	16.2	32.9
V	22	15	15	15	15	15	13	10	13
OR	22-43	60-112	86-146	129-215	172-275	224-378	318-490	413-576	499-740

F O R M R A T I O

x	0.611	0.592	0.575	0.566	0.544	0.523	0.503	0.467
s	0.070	0.051	0.048	0.037	0.048	0.031	0.032	0.029
ex	0.002	0.011	0.010	0.008	0.011	0.007	0.010	0.012
V	12	9	8	7	9	6	6	6
OR	0.44-0.73	0.53-0.73	0.50-0.65	0.50-0.65	0.41-0.63	0.47-0.57	0.44-0.55	0.44-0.52

Whorl Frequency	1	-	2	8	4	6

P. (PARAMILLERELLA) CRAIGBURNENSIS sp. nov.

Plate 16, Figs.1-5.

Description:

Test free, large, discoidal, involute, planispiral, with slight axial rotation of first whorl, typically with from $3\frac{1}{2}$ to 5 whorls, uniformly expanding, ratio decreasing from 1.82 to 1.40, with 7 or 8 chambers in first whorl, 11 or 12 in second, 14 to 16 in third, 17 to 21 in fourth, and 19 to 23 in fifth, a mean total of 52 chambers in four whorls, and 73 in five whorls; periphery broadly rounded, somewhat narrower in early whorls; umbilicus broad, shallow, deeper in specimens with slightly evolute final whorl; chambers in axial sections, broad, strongly convex lateral slopes forming single sweeping curve from umbilicus to periphery, axial ends overlapping except in final whorl, which may be slightly evolute; chambers, in sagittal sections, regularly formed, height increasing in proportion to width in later whorls, very slight peripheral lobulation; septa plane, slender, straight or slightly curved, anteriorly directed, meeting spiral wall at about 80 degrees, thickened over the tunnel by secondary deposits, mainly on posterior surface; protheca thin, (6-10 microns in final whorls) finely granular, homogeneous, thickening at intercameral

sutures; secondary deposits thick, basal layer up to three or four times the thickness of the protheca, extending high up septa but not reaching roofs of chambers in median zone of test, chomata massive, asymmetrical, distinct throughout test, tapering from steep inner face into polar ends of chambers; aperture semi-circular to lunate slit, about one third height of chamber, height reduced in tunnel by basal deposits; tunnel path irregular; proloculum spherical, large, smaller in forms with oblique first whorl.

Dimensions:

See Tables 29 and 30 below.

Holotype P.469/72.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4	4½
Chambers		6	10	12	14	16	19	22	24
Diameter	34	103	146	189	249	318	404	499	619

Depository:

Hunterian Museum of the University of Glasgow, P.469/1-114 on rock slices Nos.322A/2, 4-9 & 11; 322/2,3,7 & 10; 322B/1,2, & 8; 286C; 286C/3; 297; 297/2, & 3; 318/2 & 6; 325/3 & 4; 326/A; 326A/1,3 & 5; 328/3; 330/5; 331/A; 336; 337/3,7-9 & 13; 337A/1,3 & 5: 339/6,8,10 & 11; all from Plean Limestone position 65ft. above the Calmy Limestone, Upper Limestone Group,

Namurian of Scotland, at Craigburn, Uddington, Nr. Douglas, Lanarkshire.

Comparison and Affinities:

Of the described species of Paramillerella this species resembles most closely P. circuli Thompson in general character of the test, form ratio, and chamber count. However, it differs particularly in the more rapid expansion of its spiral, giving larger diameters at each whorl, and in its more massive and prominent secondary deposits and chomata. P. craigburnensis is similar to P. hemisphaerica sp. nov., but it has a much lower form ratio, more chambers in the earlier whorls, and a smaller diameter at any given whorl. It is closely related to P. radiata (Brady) and P. involuta sp. nov., forming a lineage in which, in a relatively short stratigraphic range, from Orchard Limestone to the Plean Limestone, a progressive increase can be observed in proloculum diameter, diameter at any given whorl, chamber count, and axial length. Nevertheless, P. craigburnensis can be easily distinguished from the related species by its larger size and greater chamber count.

Preservation and Matrix:

Preservation of this species is excellent, and the wall structure can be well observed, with the finely

granular, homogeneous protheca readily distinguishable from the lighter, apparently more coarsely granular secondary deposits. A peculiar feature of a number of specimens is the manner in which the basal deposits extend beyond the last chamber for up to threequarters of a whorl. This does not result from the recrystall-:isation of the final whorl. The final chamber of two specimens (Plate 16, figs.4 & 5) suggests that the last whorl may have been broken away, but it is a little surprising not to find any indication of its former presence such as can be found in specimens of P. hemisphaerica (Plate 17, figs.1 & 5).

Horizon and Facies:

This species is known to occur, so far, only at the Plean Limestone position, and it is recognised with certainty only at its type locality. Oblique random sections suggest its presence at equivalent horizons elsewhere in the Midland Valley, but it has not been possible to confirm this identification through lack of material.

TABLE 29

C H A M B E R S

	Prol.	1		2		3		4		5
N	59	59	59	59	59	57	50	44	21	14
x		7.31	9.9	11.53	13.34	14.86	16.64	18.25	20.0	21.21
s		0.53	0.75	0.83	1.28	1.43	1.62	1.86	1.31	1.70
ex		0.07	0.10	0.11	0.17	0.19	0.23	0.38	0.29	0.45
V		7	8	7	10	10	10	10	7	8
OR		6-9	9-12	10-14	10-17	11-18	13-21	13-22	18-24	19-25

D I A M E T E R

x	36	98	135	179	235	298	380	483	563	673
s	7	13	19	25	31	45	58	67	81	96
ex	0.8	1.7	2.5	3.3	4.1	5.9	8.3	10.1	17.8	25.5
V	18	14	14	14	13	15	16	14	14	14
OR	26-52	69-129	95-172	120-224	155-284	189-387	241-516	284-628	353-714	430-800

Spiral Ratio	1.82	1.74	1.66	1.62	1.62	1.48	1.40
Whorl Frequency	2	7	6	23	7	13	

TABLE 30

A X I A L L E N G T H

	Prol	1		2		3		4		5
N	55	55	55	55	55	55	52	40	24	8
x		59	81	105	137	174	218	263	292	332
s		10	12	15	21	23	30	37	25	39
ex		1.3	1.6	2.0	2.8	3.1	4.1	4.3	5.2	13.7
V		16	15	14	15	13	14	10	9	12
OR		43-86	60-120	77-146	95-198	129-232	155-310	215-327	258-344	301-387

D I A M E T E R

x	37	93	129	173	229	294	383	479	573	667
s	6	12	19	26	33	40	59	70	68	75
ex	0.8	1.6	2.6	3.4	4.5	5.3	8.2	11.1	14.0	26.6
V	15	13	15	15	14	14	15	15	12	11
OR	26-52	69-129	95-189	120-249	155-327	206-421	267-576	335-688	421-722	525-783

F O R M R A T I O

x	0.639	0.625	0.609	0.604	0.590	0.572	0.555	0.516	0.500
s	0.047	0.042	0.037	0.039	0.037	0.040	0.047	0.042	0.053
ex	0.006	0.006	0.005	0.005	0.005	0.006	0.007	0.009	0.019
V	7	7	6	7	6	7	8	8	11
OR	0.55-0.73	0.55-0.71	0.53-0.69	0.52-0.72	0.52-0.67	0.46-0.67	0.45-0.64	0.45-0.63	0.44-0.59

Whorl Frequency				3	12	16	16	8

P. (PARAMILLERELLA) HEMISPHAERICA sp. nov.

Plate 16, Figs.6-9. Plate 17, Figs.1-6.

Description:

Test free, large, discoidal, to nautiloid, planispiral and involute, but with slight axial rotation of first whorl, typically with from $3\frac{1}{2}$ to $4\frac{1}{2}$ whorls, uniformly expanding, spiral ratio decreasing from 1.87 to 1.52, with 7 chambers in first whorl, 10 or 11 in the second, 13 to 15 in the third, and 17 to 19 in the fourth, a mean total of 50 chambers in four whorls or probably 72 in five; periphery broadly rounded, slightly keeled in early whorls, but with strongly convex lateral slopes, in later whorls semi-circular; umbilicus shallow, wide, deeper in specimens showing slightly evolute final whorl; in axial sections chambers broad, lateral slopes becoming increasingly convex throughout growth, in final stages chambers almost circular, axial ends distinctly over-:lapping in early whorls, slightly withdrawn in last whorl; in sagittal sections chambers equidimensional in early whorls, (ratio of width to height 1) becoming increasingly rectangular, higher and narrower in later whorls, (ratio 0.3-0.5), typically with a number of narrow irregularly formed chambers; septa plane, irregularly anteriorly directed, especially in later

whorls, septal ends thickened by secondary material on both anterior and posterior surfaces, must prominent on the latter surface; protheca thin, dark, finely granular homogeneous, thickening at intercameral suture; secondary deposits thick, basal layer up to three times thickness of wall, extending high up septa but not usually reaching roofs of chambers in median zone of test, chomata present, massive, asymmetrical, distinct throughout test, steep inner surface, outer surface tapering gently into poles of chambers; aperture low, semi-circular slit; tunnel path commonly irregular, approximately quarter height of chamber; proloculum large, spherical.

Dimensions:

See Tables 31 and 32 below.

Holotype No.P.470/109.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4
Chambers		7	11	12	15	17	20	21
Diam. in Microns	47	129	172	241	318	396	499	602

Depository:

Hunterian Museum of the University of Glasgow, P.470/1-137 on rock slices Nos.311/1-10 from the Plean limestone position 49 ft. above base Calmy Limestone at 1099 ft. to 1114 ft., Upper Limestone Group, Namurian,

from Beoch Bore, Beoch Farm, New Cumnock, Ayrshire.

Comparison and Affinities:

This is the largest described species of Paramillerella with rare specimens of 5½ whorls attaining a diameter of 1 mm. It has the same type of test as Paramillerella circuli Thompson or Paramillerella protvae Rauser-Chernoussova, but it is considerably larger than either of these species. It resembles most closely Paramillerella craigburnensis sp. nov., but can be separated by its greater form ratio, larger diameter and fewer chambers at each whorl, and more irregular septation in final whorls.

Preservation and Matrix:

Crushing, collapse, and recrystallisation of part or whole of the final whorl are common features of the preservation of this species. (Plate 17, figs.1 & 5). Thus the mensurable range of specimens from 3½ to 4½ whorls is low. A population of complete specimens would probably range from 4 to 5 whorls. While some distortion or crushing of the final whorl of Paramillerella is common, in this case, it is mainly due to the reworked and partially brecciated nature of the host sediment.

Horizon and Facies:

This species has been recorded, so far, only from

the Plean Limestone position 49ft. above the Calmy Limestone, Upper Limestone Group, Namurian, from 1099ft. to 1114ft. in Beoch Bore, Beoch Farm, New Cumnock, Ayrshire. It occurs in finely bioclastic micrites, which are partially reworked, recrystallised and brecciated, and it is closely associated with the highly distinctive coral assemblage of this position.

TABLE 31

C H A M B E R S

	Prol.	1		2		3		4		5
N	76	76	76	76	76	76	61	41	25	4
x		7.09	9.21	10.88	12.53	14.25	15.13	18.12	20.04	21.75
s		0.61	0.69	0.72	0.95	1.22	1.56	1.29	1.18	
ex		0.07	0.08	0.08	0.11	0.14	0.2	0.2	0.24	
V		9	8	7	8	9	10	7	8	
OR		6-8	8-11	9-12	11-15	12-17	13-19	16-21	18-22	21-23

D I A M E T E R

x	38	110	152	206	268	351	445	553	679	
s	6	13	17	23	26	35	43	53	62	
ex	0.7	1.5	2.0	2.6	3.0	4.0	5.5	8.3	12.4	
V	15	12	11	11	10	10	10	10	9	
OR	26-52	86-138	120-181	172-258	215-335	267-430	335-542	413-645	507-757	645-826

Spiral Ratio		1.87	1.76	1.70	1.66	1.57	1.52	
Whorl Frequency				15	20	16	19	3

TABLE 32

A X I A L L E N G T H

	Prol.	1		2		3		4		5
N	50	50	50	50	50	48	44	36	24	5
x		64	95	127	167	218	274	325	383	396
s		9	11	17	20	25	29	40	44	32
ex		1.3	1.6	2.4	2.9	3.6	4.4	6.6	9.1	14.1
V		14	12	13	12	11	11	12	11	8
OR		52-77	69-120	95-155	120-206	163-267	215-344	258-421	310-473	361-447

D I A M E T E R

x	39	103	143	194	257	338	435	541	674	725
s	7	12	16	21	30	37	48	59	84	87
ex	1.0	1.7	2.2	3.0	4.2	5.3	7.3	9.9	17.1	38.7
V	17	12	11	9	12	11	11	11	12	12
OR	26-56	86-129	120-172	155-232	198-327	258-421	327-359	413-636	516-808	645-834

F O R M R A T I O

x	0.626	0.662	0.654	0.648	0.645	0.63	0.603	0.573	0.55
s	0.046	0.045	0.051	0.054	0.046	0.043	0.049	0.039	0.037
ex	0.007	0.006	0.007	0.008	0.007	0.007	0.008	0.008	0.017
V	7	7	8	8	7	7	8	7	7
OR	0.54-0.75	0.57-0.76	0.55-0.78	0.49-0.80	0.58-0.77	0.55-0.72	0.50-0.67	0.50-0.66	0.49-0.59

Whorl Frequency	2	4	8	12	19	4

P. (PARAMILLERELLA) WESTERWOODENSIS sp. nov.

Plate 15, Figs.7-14. Plate 19, Fig.2.

Description:

Test free, discoidal, involute, planispiral, but often with some axial rotation of first whorl, characteristically with from $3\frac{1}{2}$ to $4\frac{1}{2}$ whorls, more tightly coiled in the early whorls, but spiral ratio dropping slowly from 1.87 to 1.6, with 7 chambers in the first whorl, 10 or 11 in the second, 13 or 14 in the third, and 14 to 16 in the fourth, a mean total of 46.5 chambers in four whorls; periphery broadly rounded in early whorls, narrowly rounded in outer whorls, umbilicus narrow, shallow to deep, deeper in specimens showing slight evolution of final whorl; chambers in axial sections with convex lateral slopes in early stages, becoming progressively flatter in outer whorls, and sweeping into umbilicus in broad curve, axial ends overlapping except in final half whorl of large specimens; chambers in sagittal sections showing negligible peripheral inflation, chambers quadrate in first whorl, thereafter becoming rectangular, strongly so in outer whorls, where ratio of height to width may fall to 0.5; septa plane, almost straight in early whorls, becoming long, curved in outer whorls, slightly anteriorly directed, meeting spiral wall at an angle from 75-90 degrees, often

with slight terminal thickening by secondary material over tunnel; protheca thin (6-10 microns), dark, finely granular; secondary deposits rather thin, basal layer about twice thickness of protheca, chomata poorly developed, variable from platform-like modifications of the periphery to low asymmetrical levees, tapering towards poles of the chambers, sometimes absent in last whorl, aperture low slit, possibly enlarged in tunnel; tunnel path normally regular; proloculum spherical, large.

Dimensions:

See Tables 33 and 34 below.

Holotype P.471/13.

Whorl No.	Prol.	1	1½	2	2½	3	3½
Chambers		7	9	11	12	13	15
Diameter	30	86	120	172	224	301	396

Depository:

Hunterian Museum of the University of Glasgow on rock slices 1143/1-10, 1146/2-3, 1144/1-4, 1142/4, and thin sections 1144D. 1145A, 1143, 1143CT. 1143/DT, and 1142, all from Castlecary Limestone, Westerwood Quarry, Nr. Castlecary, Dumbartonshire.

Comparison and Affinities:

This species is similar to P. (P.) bigemmicula

Igo in the general shape of the test, development of secondary deposits, and peripheral contour, but can be differentiated from that species by its more involute umbilicate test with higher from ratio, and more rapidly expanding spiral in later whorls. P. (P.) westerwoodensis like P. (P.) bigemmicula is similar to Millerella marblensis, particularly in the development of long arcuate septa in final whorl, but it shows only the slightest indication of uncoiling of the final whorls, and a much higher form ratio than the involute stage of Millerella marblensis.

P. (P.) advena and P. (P.) ampla Thompson are similar to P. (P.) westerwoodensis in having narrowly rounded periphery, and flat lateral slopes, but these species do not approach P. (P.) westerwoodensis in diameter of the proloculum, rate of expansion of the spiral, and the distinctly smaller form ratio.

Preservation and Matrix:

Occurring in strongly dolomitised limestones, the wall of this species shows an appreciable degree of recrytallisation, and is much coarser grained, lighter in colour, and less homogeneous than the wall structure observed in typical specimens of Paramillerella from other horizons in the Upper Limestone Group. This alteration commonly leads to an accentuation of the

layered structure of the wall, commonly emphasising the interface between protheca and epitheca (Plate 3, figs.2 & 3), to produce a 'tectum'. A specimen in an advanced state of recrystallisation is shown in Plate 4, fig.2, and here it can be seen that even the secondary layering is obliterated by crystal growth.

In comparison with other Upper Limestone Group species P. (P.) westerwoodensis differs in more narrowly rounded periphery and low form ratio. It resembles P. (P.) indicis most closely in dimensions of the test, but differs markedly in chamber count, and while it has a similar chamber count to P. (P.) involuta, it differs significantly in dimensions and form ratio.

Horizon and Facies:

A common and typical form in the Castlecary Limestone, the uppermost horizon of the Upper Limestone Group, this species occurs in greatest numbers in the slightly argillaceous, strongly bioclastic, phases of the limestone. It is often quite rare in some of the strongly algal micritic phases. This species, or a closely allied form, occurs in the Plean position at localities in South Ayrshire, and it has been recorded also from equivalent horizons in the North of England.

TABLE 33

CHAMBERS

	Prol.	1	1½	2	2½	3	3½	4	4½
N	31	31	31	31	30	28	25	16	-
x		6.84	8.91	10.42	11.77	13.18	14.88	16.06	
s		0.51	0.74	0.79	0.67	0.85	0.92	1.09	
ex		0.09	0.13	0.14	0.12	0.16	0.18	0.27	
V		8	8	8	6	6	6	7	
OR		6-8	8-12	9-12	11-13	11-16	13-17	14-18	-

DIAMETER

x	27	79	109	148	196	266	347	426
s	4	8	12	16	22	30	48	37
ex	0.8	1.5	2.2	2.9	4.0	5.0	9.6	9.1
V	15	10	11	11	11	11	14	9
OR	17-72	69-103	95-146	129-189	163-258	206-361	258-473	353-490

Spiral Ratio		1.87	1.79	1.79	1.77	1.60
Whorl Frequency		1	2	3	9	16 -

TABLE 34

A X I A L L E N G T H

	Prol.	Whorl No. 1	1½	2	2½	3	3½	4	4½
N	12	12	12	12	12	12	11	8	3
x		39	51	71	97	131	157	186	
s		6	8	12	20	27	13	18	
ex		1.7	2.2	3.5	5.9	7.8	4.0	6.5	
V		15	15	17	21	21	9	10	
OR		34-52	43-69	60-103	69-146	86-198	120-181	163-224	172-241

D I A M E T E R

x	28	70	97	129	176	237	306	410	
s	4	7	13	18	29	40	36	40	
ex	1.1	2.0	3.7	5.3	8.3	8.9	8.8	9.1	
V	16	10	13	14	16	17	12	10	
OR	17-30	60-86	77-129	95-181	129-249	181-335	241-378	310-473	430-550

F O R M R A T I O

x	0.569	0.526	0.553	0.547	0.555	0.512	0.463	
s	0.056	0.047	0.056	0.033	0.040	0.034	0.042	
ex	0.016	0.014	0.017	0.009	0.011	0.010	0.015	
V	10	9	10	6	7	7	9	
OR	0.50-0.63	0.45-0.60	0.50-0.64	0.50-0.61	0.48-0.61	0.45-0.57	0.40-0.53	

Whorl Frequency				1	3	5	3

Family S T A F F E L L I D A E Miklukho-Maklay, 1949.

Genus PSEUDOENDOTHYRA Mikhailov, 1939, emended.

Fusulinella: Moeller, 1877 and 1878 (pars).
Colani, 1924 (pars).

Staffella: Dutkevitch, 1934 (pars)
Rauser-Chernoussova-Beljaev-Reitlinger, 1936 (pars).

Pseudoendothyra: Mikhailov, 1939.
Miklukho-Maklay, Rauser-Chernoussova and Rozovskaya, 1959.
Grozdilova & Lebedeva, 1960.
Boghush & Juferev, 1962.
Rozovskaya, 1963 (pars).

Parastaffella: Rauser-Chernoussova, 1948 (non Rauser-Chernoussova, 1949 and Rauser-Chernoussova & Dalmatskaya, 1954).
Vissarionova, 1948.
Rauser-Chernoussova et al, 1951 (pars).
Grozdilova & Lebedeva, 1950 and 1954 (pars).
Schlykova, 1951.
Putrya, 1956 (pars).
Ganelina, 1956.
Golubstov, 1957.
Durkina, 1951.

Nankinella: Thompson & Miller, 1944 (non Lee, 1933).
Thompson, 1947, 1948 (pars) and 1964 (pars).
Igo, 1957 (pars).
Toriyama, 1958 (pars).

Eoparastaffella: Vdovenko, 1954.

Paramillerella: Igo, 1957 (pars).

Ozawainella: Grozdilova & Lebedeva, 1954 (pars).

Type Species:

Fusulinella struvii Moeller, 1879, p.31-36.
Plate 2, figs.1a-c; Plate 5, Figs.4a-c.

Description:

Test lensoid, or discoid, planispiral, but with first whorl sometimes showing slight irregularity in coiling, broad, shallow, to narrow deep umbilicus; periphery typically rounded in early whorls, becoming angular to keeled in later whorls; aperture basal, low semi-circular or lunate slit; wall thick, recrystallised or replaced, structure indefinite, proportedly four layered, diaphanotheca, tectum and lower and upper tectoria; secondary deposits normally thin, basal deposit sparse, absent in equatorial zone of test, pseudochomata well developed, possibly weak chomata; septa plane, long straight, usually strongly differentiated from slightly lobulate external wall.

Comparison and Affinities:

This genus was proposed by Mikhailov (1939), and based on the species Fusulinella struvii Moeller, 1879, with the individual Plate V, fig.4c, as type. Subsequently, Rauser-Chernoussova (1948) erected a new genus Parastaffella based also on the species Fusulinella struvii, but with a different individual as type (Moeller, 1879, Plate V, fig.4b) and she argued that, since Mikhailov had included, within his material, forms referable to other Carboniferous genera (Ozawainella, and Eostaffella) and placed them together only because of the common character of a keeled periphery, the genus was effectively invalid. Furthermore, Mikhailov considered that the diaphanotheca was not always present in the type species, while Rauser-Chernoussova suggested that a four layered wall with a thick clear diaphanotheca was diagnostic. However, despite the demerits of Mikhailov's understanding and interpretation of his own new genus, its type species is conspecific with that of Parastaffella and, thus, Pseudoendothyra retains priority as has been recognised by Miklukho-Maklay, Rauser-Chernoussova and Rozovskaya, 1959, and others subsequently, with the specimen Fusulinella struvii Moeller, 1870, Plate V, fig.4b, as type.

The recognition of primitive forms of this genus

rests basically on its wall structure for in the general morphology of the test it is an isomorph of Paramillerella. The nature of the staffellid wall has been discussed above and the difficulties of recognising such a structure outlined. Whether this wall is different from that of the ozawainellids in underlying fine structure is dubious, and certainly, the recognition of four layers in Pseudoendothyra seems highly speculative considering the recrystallised nature of the wall in typical specimens. More advanced forms may be recognised by means of certain distinctive morphological features such as, the typically keeled periphery with rather flat or only slightly convex lateral slopes, the thick wall with very sparse basal deposits, which are commonly absent over the equatorial zone of the test, and the long thick wedge-like septa tapering from the periphery in sagittal sections.

The staffellid genera are conservative in test shape and internal morphology such that the phylogenetic trend to increase the volume of protoplasm is achieved mainly by increasing the number of whorls in the test. As a result there is no clear cut morphological change between Pseudoendothyra and related genera.

Pseudoendothyra is differentiated from Staffella by means of its smaller lensoid or discoid test with usually no more than 5½ whorls, and, as interpreted

here excludes spherical to subspherical forms such as Parastaffella fraudulenta and P. keltmensis Rauser-Chernoussova, 1949, which are assigned to Staffella on the basis of their broadly rounded inflated form.

Nankinella is distinguished from Pseudoendothyra on the basis of its larger multivolute test with non-:umbilicate, inflated polar ends. The smaller umbilicate forms assigned to Nankinella such as, Nankinella plummeri Thompson, 1947, or Nankinella nagatoensis Toriyama, 1958, are refered to Pseudoendothyra for, apart from slightly greater dimensions, there is no morphological character which would distinguish then from the latter genus.

Preservation and Matrix:

As is discussed above, the wall of this genus is, most characteristically, diagenetically altered, and shows a sensitivity to such changes very much greater than contemporary ozawainellid genera. Study of the material from the Scottish Carboniferous suggests that the four layered wall, commonly attributed to these forms, results fundamentally form the alteration of the wall, and that the contrast in the walls lies in the underlying chemical composition rather than the structure.

The supposed diaphanotheca develops through grain growth within the crystalline material of the

wall itself, and the larger crystals do not absorb the light in the manner of more homogeneous, finely granular material. Thus the wall is grey and translucent, but its contacts with the infilling of the test are frequently marked by a very thin darker zone which, in this case, cannot be proved to represent more than the interface between the wall and the drusy calcite infilling of the test (Plate 7, fig.1). The dark zone is no more prominent than the boundaries between many of the larger crystals, and it is a striking feature of the preservation that, where the wall is in contact with the microcrystalline matrix its boundaries can scarcely be discerned, yet they are quite sharply defined against the drusy infilling. It is possible to examine the distribution of the secondary deposits and these are confined exclusively to the base of the chambers and the lower ends of the septa. They do not at any time extend onto the roofs of the chambers. There is, therefore, no evidence in any of the material examined to suggest that the wall had a tectum or lower tectoria, although there are frequently darker zones in the wall at these positions.

Horizon and Facies:

Pseudoendothyra is listed as a Carboniferous to Lower Permian form by Miklukho-Maklay, Rauser-Chernoussova

and Rozovskaya, 1959, but it would seem that the Permian records are based on material which is more correctly assigned to the genus Staffella. Appearing first in the Lower Visean, the genus reaches its maximum abundance during Middle Visean times and continues with diminishing frequency into the Middle and Upper Carboniferous. Its distribution is world wide.

PSEUDOENDOTHYRA DIAPHANA sp. nov.

Plate 18, Figs.1-5.

Description:

Test free, lensoid, involute, planispiral, first whorl commonly showing slight deviation in coiling, usually with $3\frac{1}{2}$ to $4\frac{1}{2}$ whorls, typically the first whorl with 7 chambers, the second whorl with 11, third whorl with 13-15, and fourth with 15-18, weakly umbilicate; periphery in early whorls broadly rounded, becoming more angular and keeled in outermost whorls; chambers with rather flat lateral slopes curving sharply into umbilicus, giving spwar shaped axial sections; in sagittal sections, chambers proportions changing throughout spire, width decreasing in proportion to height, with ratio 1 in first whorl, 0.4 to 0.6 in final whorl, very little peripheral inflation except in last half whorl; septa plane, straight, slightly anteriorly directed, long but characteristically wedge-line, or tapering from periphery, joining spiral wall almost at right angles; wall thick, up to 0.05mm., grey translucent, recrystallised; thin secondary deposits, thickening septal sutures from tunnel towards axial ends of chambers, absent over periphery of each whorl, (pseudochomata); aperture low, basal lunate slit, about one fifth the height of chamber; proloculum spherical.

Dimensions:

See Tables 35-36 below.

Holotype, P.461/3.

Whorl No.	Prol.	1	1½	2	2½	3	3½	4
Chambers		7	10	12	13	14	14	15
Diameter	43	112	155	215	284	396	533	679

Depository:

The Hunterian Museum of the University of Glasgow, P.461/1-50 on rock slices Nos.145/1-6 and 144/1-4 from Index Limestone, Upper Limestone Group, Namurian, of Poniel Water Coalburn, Lanarkshire.

Comparison and Affinities:

Comparison with other species is difficult because, with few exceptions, they are based on a small number of axial sections. The systematic significance of chambers and septa in sagittal sections and the inadequacies of axial sections (Burma, 1948 p.759) are generally ignored. The result is that knowledge of the mean or modal characters of the species, or their range of variation, is minimal. However, despite these limitations the following comparisons are made.

In general test shape this species resembles most closely Pseudoendothyra bona Rozovskaya, but can be differentiated from this species by its more rapidly

expanding spire with 4 whorls and 49 chambers in a test of 0.61 mm. diameter, as opposed to 5 whorls and 65 chambers in a test of 0.64 mm. in P. bona. In the lenticular form of the test, with rounded periphery in the earliest whorls, P. diaphana resembles P. concinna (Schlykova), but it can be differentiated by its more rapidly expanding spiral, involute coiling, and shallow umbilicus. There is a superficial resemblance to P. composita (Dutkevitch) but this is a more evolute slender shell than P. diaphana with a keeled periphery throughout growth.

P. diaphana is differentiated from contemporaneous species of Paramillerella and Eostaffella by the recrystallised wall structure, but there are, in addition, a number of characters which distinguish this species; (Text fig.24, 26); the keeled periphery with almost flat lateral slopes; lack of thick basal deposits and chomata; very rapid expansion of the spiral; strongly rectangular chambers in later whorls, with long straight tapering septa.

Preservation and Matrix:

Characteristically the wall of this species is recrystallised, grey and diaphanous, the boundaries of the crystals of the drusy infilling commonly transect the septa and cross the spiral wall of the interior.

The boundary of the external wall cannot be clearly distinguished from this matrix. The host sediment has suffered a marked degree of recrystallisation and dolomitisation, yet adjacent species of Endothyra, Endostaffella and Paramillerella, retain their fine grained, dark, homogeneous granular wall (Plate 7, fig.2).

Horizon and Facies:

Found, so far, only in the Index Limestone, lowermost horizon of the Upper Limestone Group, Namurian of Scotland, where it occurs abundantly, but in a restricted facies. It is typically absent in the more argillaceous phases of the limestone, and has been found in a relatively narrow band of patchily sparry, bioclastic micrites at only two localities. Its appearance in the limestone is associated with the occurrence of Globivalvulina globulus sp. nov. and Bradyina samarinaformis sp. nov.

TABLE 35

CHAMBERS

	Prol.	1	2		3		4	5
N	28	28	28	28	28	22	9	4	-
x		7.25	9.19	10.81	12.29	13.53	14.86	16.0	
s		0.43	0.57	0.6	0.92	1.15	1.42	1.73	
ex		0.08	0.11	0.11	0.17	0.22	0.30	0.58	
V		6	6	6	7	8	10	11	
OR		7-8	8-10	10-12	11-15	11-16	12-18	13-18	17-19

DIAMETER

x	38	111	154	215	279	388	490	610
s	7	15	23	34	45	63	65	106
ex	1.3	2.9	4.3	6.5	8.5	11.9	13.8	35.3
V	18	14	15	16	16	16	13	17
OR	26-52	86-146	120-206	163-292	224-370	292-506	378-602	481-800

Spiral Ratio	1.92	1.83	1.80	1.75	1.56

Whorl Frequency	6	13	5	4

TABLE 36

A X I A L L E N G T H

	Prol.	1		2		3		4		5
N	21	21	21	21	21	21	21	17	7	1
x		58	86	111	146	186	235	285	342	
s		8	12	16	19	20	29	28	44	
ex		1.7	2.7	3.4	4.2	4.4	6.3	6.9	16.8	
V		14	14	14	13	11	12	10	13	
OR		43-77	69-120	86-155	112-189	146-224	181-301	215-344	258-387	404

D I A M E T E R

x	35	95	133	192	244	329	431	543	668	
s	5	13	18	28	32	39	48	59	87	
ex	1.2	2.8	4.0	6.2	6.9	8.6	10.3	14.6	32.7	
OR	26-43	77-129	112-181	146-249	198-327	258-447	344-550	430-671	550-783	731
V	15	14	14	15	13	12	11	11	13	

F O R M R A T I O

x		0.617	0.639	0.613	0.594	0.575	0.546	0.528	0.511	
s		0.055	0.068	0.041	0.044	0.045	0.043	0.043	0.044	
ex		0.012	0.015	0.009	0.010	0.010	0.009	0.010	0.017	
V		9	11	7	7	8	8	8	9	
OR		0.50-0.70	0.50-0.79	0.52-0.68	0.52-0.71	0.48-0.67	0.47-0.65	0.45-0.62	0.47-0.59	

Whorl Frequency							4	10	6	1

Subfamily BRADYININAE Reitlinger, 1950.

Test nautiloid to globose, almost planispiral, involute; septa simple or complex with additional laminae formed by outgrowths of the wall on the anterior and posterior of the septa; aperture simple basal or complex cribrate, with supplementary sutural pores; wall finely perforate to coarsely alveolar, with varying amount of calcareous adventitious agglutinate material.

Genus BRADYINA Moeller, 1878.

BRADYINA SAMARINAFORMIS sp. nov.

Plate 20, Figs.2 & 3.

Description:

Test free, relatively large, nautiloid, subspherical, planispiral involute, very slightly umbilicate, usually $2\frac{1}{2}$ or, more rarely, 3 whorls present, increasing very rapidly in height, completely embracing throughout; with 4 chambers in first whorl, 5 or 6 in second whorl, and typically with 5 or 6 in final whorl, total chambers in adult test from 10 to 16; periphery broadly rounded, flattening and steep-:ening as it curves into lateral slopes; chambers inflated globose, apertural face slightly less convex than spiral wall, but joining it in broad sweeping curve; sutures depressed, distinct, sub-limbate, perforate; septa complex, formed by pre-septal and post-septal laminae, and resorbed remnant of apertural face, post-septal laminae of each chamber linking across end of resorbed margin of apertural face with pre-septal laminae, but perforated to allow communication with sutural pores, pre-septal and post-septal laminae of each chamber unite in basal lateral part of chamber cutting off umbilical extremities; interlamellar cavity present at least from second chamber, attaining width 100 microns at second whorl, 250 microns in final

whorl; septal opening about half height of chamber; wall thin, very finely alveolar, composed of finely granular calcite without agglutinate particles; alveoli from 2-4 microns, constricting at exterior, forming darker more continuous layer (tectum); aperture cribrate shield, pores opening between wedge-like inward tapering portions of apertural face, with subsidiary sutural pores of similar character; proloculum large, spherical.

Dimensions:

Holotype, P.450/2.

Whorl No.	Prol.	1	2	Final
Chambers		4	5	5 (12)
Diameter in microns.	112	387	1281	1703
Wall thickness in microns.		17	34	43

For complete data see Tables 37-39 below.

Depository:

Hunterian Museum of the University of Glasgow,. Holotype P.450/2 and Paratypes P.450/1 and P.450/3-25, on rock slices 144/1-8 and 145/11, all from Index Limestone, Poniel Water, Coalburn, Lanarkshire.

Comparison and Affinities:

This species is closely similar to Bradyina concinna Reitlinger in the number of chambers per whorl, but it differs in having a wall about half as thick as B. concinna, and a slightly higher form ratio. The slenderness of the wall of B. samarinaformis and its general morphology suggests that it is very closely related to Janischewskina typica Mikhailov, but it differs from that species in having a thicker wall with distinct, though very fine, alveolar structure. In his study of the Middle Carboniferous bradyinids, Reitlinger (1950 p.39) recognised three broad morphological groups. In the first group were included large bradyinids with thick coarsely alveolar walls, and a relatively large number of chambers. From this first major group two sub-groups were recognised; species with a narrow interseptal space developed from the first chamber (B. nautiliformis Moeller, B. eonautiliformis Reitlinger, B. pseudonautiliformis Reitlinger), and species with a wide interseptal space (B. cribrostomata Rauser-Chernoussova & Reitlinger, B. magna Roth & Skinner). It was noted by Reitlinger (1950 page 39), that B. concinna differed from the typical species of the sub-groups in having large dimensions, but a comparatively thin wall, and a smaller number of chambers, and he, therefore, suggested

that B. concinna may have been the ancestor of Glyphostomella and the closely associated group of species B. samarica Reitlinger and B. lepida Reitlinger. Such a phylogeny for these species seems plausible, and it is, therefore, possible to suggest that Glyphostomella develops from Janischewskina through species such as B. samarinaformis sp. nov. and B. concinna by progressive reduction in number of chambers, and slight increase in thickness of the wall.

Horizon and Facies:

B. samarinaformis occurs abundantly in a single band a few inches thick at its type locality, and it has so far been found in the Index Limestone only at one other locality. It is associated with Globivalvulina globulus, and Pseudoendothyra diaphana, species which also have a restricted vertical and geographical distribution in the Index Limestone (Text fig.17).

Statistics:

See Tables 37 to 39.

TABLE 37

Population from Index Limestone, Poneil Water, Coalburn, Lanarkshire.

C H A M B E R S

Whorl No.	Prol.	1	2	Final Whorl at Chamber 10	12	15
N	17	17	12	7	4	2
x		4	5.25			
s		0	0.59			
ex		0	0.17			
V		0	11			
OR		4	4-6	5	5	6

D I A M E T E R

x	105	340	957	999	1,643	1,931
s	16	51	152	185	147	-
ex	4	18	36	70	73	-
V	15	14	16	18	9	-
OR	77-129	215-421	654-1,281	851-1.273	1,429-1.754	1,797-2,064

TABLE 38

THICKNESS OF WALL

Whorl No.	Prol.	1	2	Final Whorl at Chamber 10	12	15
N	17	17	16	7	4	2
x		19	33	36	41	41
s		4	5	6	4	-
ex		0.9	1.4	2.2	2.2	-
V		14	17	17	11	-
OR		9-26	26-43	26-43	34-47	39-43

TABLE 39

FORM RATIO

Whorl No.	1	1½	2	2½
N	8	8	5	2
x	0.873	0.919	0.904	0.82
s	0.136	0.101	0.13	-
ex	0.048	0.036	0.059	-
V	16	11	14	-
OR	0.61-1.02	0.76-1.12	0.85-1.14	0.77-0.86

BRADYINA PERFORATA sp. nov.

Plate 20, Fig.1. Plate 21, Figs.1-4.

Description:

Test free, relatively large, nautiloid, subspherical, planispiral, involute, very slightly umbilicate, usually $2\frac{1}{2}$, more rarely, 3 whorls, increasing very rapidly in height, completely embracing throughout, with 3 or 4 chambers in the first whorl, and 4 or 5 in the second whorl, final whorl with 5 or sometimes 6 chambers, total chambers in adult test ranging from 9-16; periphery broadly rounded with slightly flatter lateral slopes; chambers inflated globose, apertural face slightly less convex than spiral wall, but joining it in broad sweeping curve; sutures distinct depressed, perforate; septa complex, formed by pre-septal and post-septal lamellae, and resorbed remnant of apertural face, post-septal lamellae of each chamber linking across end of resorbed apertural face with pre-septal lamellae of previous chamber, but perforated to allow access to sutural pores; pre-septal and post-septal lamellae of each chamber unite in basal lateral part of chamber cutting off umbilical extremities; interlamellar cavity present at least from second or third chamber, attaining width of 100 microns at second whorl, and 260 microns at third whorl; septal opening about one third height

of chamber; wall moderately thick, up to 103 microns in final whorl, distinctly alveolar, intervening wall equal to or slightly greater than diameter of alveoli; alveoli, with diameter of 10 microns at second whorl, attain diameter of 22 microns in final whorls, and constrict sharply at exterior forming dark more continuous outer layer (tectun); aperture cribrate, slit-like pores on lower semi-circular surface of apertural face, with subsidiary sutural pores of similar character; proloculum large, spherical.

Dimensions:

Holotype, P.451 on rock slice 26A/2.

Whorl No.	Prol.	1	2	3	Final
Chambers		4	4	5	5
Diameter in microns	85	310	800	1694	2184
Wall thickness in microns.		17	52	95	103

For further data see Tables 40-44 below.

Depository:

Hunterian Museum of the University of Glasgow. Specimens from the Orchard Limestone, Holotype No.P.451, River Avon, Strutherhill, Larkhall, Lanarkshire; No.P.452 from Auldhouse Burn, Muirkirk, Ayrshire; No.P.453 from Garpel Water, Muirkirk, Ayrshire;

P.454 from River Nethan, near Auchlochan House, Lesmahagow, Lanarkshire; P.455 from Poniel Water, Coalburn, Lanarkshire; and P.456/1-2 from Lugton Water, Montgreenan, Ayrshire. Specimens Nos. P.457/1-4 from Plean Limestone, Beoch Bore, Beoch Farm, New Cumnock, Ayrshire, and P.458 from Craigburn, Uddington, near Douglas, Lanarkshire. Specimens Nos.P.459/1-5 from Castlecary Limestone, Westerwood Quarry, near Castlecary, Dumbartonshire.

Comparison and Affinities:

This species is closely similar to Bradyina cribrostomata Rauser-Chernoussova & Reitlinger, but differs from that species in having fewer chambers in each whorl, and in adult test, and also in having a consistently thinner wall with smaller pores at any given whorl. B. perforata shows some resemblance to B. concinna Reitlinger in number and size of its chambers, but can be differentiated by its more coarsely alveolar and slightly thicker wall. It can be distinguished from B. rotula Eichwald by smaller test thinner wall and smaller alveoli, and from B. potanini Venukoff by rather thicker wall, and more rapidly expanding spiral and, thus, larger test at any given whorl.

Horizon and Facies:

This species has been recorded from all the major limestone positions in the Upper Limestone Group except the Index Limestone. It is, however, extremely rare within the Lyoncross Limestone and it is known only from single fragmentary random sections at two localities, Craigburn and Kennox Water, both near Douglas, Lanarkshire. In the remaining marine horizons B. perforata occurs sporadically, usually showing greatest abundance in limestones where the argillaceous content is low.

TABLE 40

Specimens Nos. P.459/1-5 from Castlecary Limestone, Westerwood Quarry.

C H A M B E R S

W h o r l No.	Prol.	1	2	3
N	5	5	4	1
x		3.8	4.75	6
S		0.45	0.5	-
ex		0.2	0.25	-
V		12	11	-
OR		3-4	4-5	6

D I A M E T E R

	Whorl No.			Final Whorl at Chamber				
	Prol.	1	2	3	9	12	14	15	16
N	5	5	4	1	4	1	1	1	1
x	101	340	834	1,574	843	1,135	2,064	1,574	1,858
s	11	41	144	-	151	-	-	-	-
ex	5	19	72	-	76	-	-	-	-
V	11	12	7	-	18	-	-	-	-
OR	86-112	292-387	688-989	-	688-980	-	-	-	-

T H I C K N E S S O F W A L L

x	17	43	52	47	52	77	52	60
s	-	12	-	-	-	-	-	-
ex	-	6	-	-	-	-	-	-
V	-	28	-	-	-	-	-	-
OR	17	34-60	-	-	-	-	-	-

TABLE 41

Specimen Nos. P.457/1-4 and No. P.458 from Plean Limestone at Beoch, and Craigburn.

C H A M B E R S

	Whorl No.									
	Prol	1	2	3	Final Whorl at Chamber					
					9	11	12	13	15	16
N	4	4	4	2	2	1	1	1	1	1
x		4	4.75	5.5						
s		0	0.5	-						
ex		0	0.25	-						
V		0	11	-						
OR		4	4-5	5-6						

D I A M E T E R

x	84	349	811	1,793	770	1,238	1.238	1.634	1.793	2.184
s	19	43	94	-	-	-	-	-	-	-
ex	10	21	47	-	-	-	-	-	-	-
V	23	12	12	-	-	-	-	-	-	-
OR	77-120	292-396	740-946	1,634-1,952	740-800					

T H I C K N E S S O F W A L L

x	17	43	73	47	52	69	69	77	86
s	0	7	-	-	-	-	-	-	-
ex	0	5.4	-	-	-	-	-	-	-
V	0	16	-	-	-	-	-	-	-
OR	17	34-52	69-77	-	-	-	-	-	-

TABLE NO. 42

Specimen Nos. P.451-455 and P.456/1-2 from Orchard Limestone

C H A M B E R S

	Whorl No.			Final Whorl at Chamber				
	Prol.	1	2	3	9	10	11	12	14
N	6	6	6	1	1	2	2	1	1
x		3.2	4.7	5					
s		0.41	0.51	-					
ex		0.16	0.21	-					
V		13	11	-					
OR		3-4	4-5	-					

D I A M E T E R

x	85	295	740	1,694	671	1,075	1,660	1,238	2,184
s	7	38	121	-	-	-	-	-	-
ex	3	16	51	-	-	-	-	-	-
V	8	13	17	-	-	-	-	-	-
OR	77-95	232-335	585-903	-	-	920-1,238	1,625-1,694	-	-

T H I C K N E S S O F W A L L

x	24	47	95	43	73	90	77	103
s	4	9	-	-	-	-	-	-
ex	2	4	-	-	-	-	-	-
V	19	19	-	-	-	-	-	-
OR	17-26	34-60	-	-	69-77	86-95	-	-

TABLE 43

D I M E N S I O N S O F A X I A L S E C T I O N S

Whorl No.	Prol.	1	1½	2	2½	3	
Diameter	86	310	482	731			P.452
Length		224	473	602			
Ratio		0.722	0.982	0.824			
Diameter	120	292	430	671	1,075	1,634	P.456/2
Length		232	396	559	972	1,445	
Ratio		0.794	0.92	0.833	0.904	0.832	

TABLE 44

A comparison of the mean dimensions from all three horizons

	Whorl No.-				Final Whorl at Chamber No.-				
Prol	1	2	3	9	10	11	12	13	14
-	3.8	4.75	6						
-	4	4.75	5.5						
-	3.2	4.7	5						
				DIAMETER					
101	340	834	1,574	843	-	-	1,135	-	2,064
84	349	811	1,793	770	-	1,238	1,634	1,238	-
85	295	740	1,694	671	1,075	1,625	1,238	1,694	2,184
				THICKNESS OF WALL					
	17	43	52	57	-	-	52	-	77
	17	43	73	47	-	52	69	69	-
	24	47	95	43	73	90	77	-	103

The dimensions are listed in stratigraphic order

Castlecary - Plean - Orchard.

Genus ENDOTHYRANOPSIS Cummings, 1955.

ENDOTHYRANOPSIS SPHAERICA (Rauser-Chernoussova Beljaev & Reitlinger), 1936.

Plate No.21, Figs.5 to 8.

Endothyra crassa Moeller, 1878, pp.146-150,
Plate IV, fig.2a-c; Plate XII,
figs.1a & 1b.
Moeller, 1879, pp.19-20.

Endothyra crassa var. sphaerica Rauser-Chernoussova, Beljaev & Reitlinger 1936, pp.209-240,
Plate VI, fig.4.
Rauser Chernoussova, 1948, p.168,
Plate IV, fig.1.
Grozdilova & Lebedeva, 1954, pp.92-93,
Plate XI, figs.5-6.
Durkina, 1959, pp.184-185, Plate XIII
figs.1,2. Plate XIV, fig.1.

Endothyranopsis crassus var. sphaerica Grozdilova & Lebedeva, 1960, p.77, Plate VII, fig.2.

Endothyranopsis crassa subsp. sphaerica Rozovskaya, 1963, pp.56-57, Plate VII, fig,2,3.
Plate IX, figs.1-2.

Remarks:

Rauser-Chernoussova (1948 pp.170-174) compared the dimensions of adult specimens of Endothyranopsis at successive zones in the Visean of Russia and showed that there was an increase in diameter, number of chambers and form ratio, from the Tula zone to the lower Namurian, Protvin zone. The most significant change is in form ratio which reflects the expansion in axial length from the more primitive species E. intermedia Rauser-Chernoussova of the Tula and Aleksin zones to E. sphaerica of the Taruss, Steshev, and Protvin zones of the upper Visean and lower Namurian. All of the measurements were based on the final whorl of specimens many of which are not in truly axial or sagittal orientations and, therefore, the ratio of diameter to length (form ratio) is exaggerated. Moreover, in many instances random sections refered to Endothyronopsis sphaerica appear to be based on oblique axial sections of E. crassa. The change in dimensions described by Rauser-Chernoussova does occur, but can be more precisely defined by the study of more accurately orientated sections. In the Upper Limestone Group few individuals attain the size of the species discussed by Rauser-Chernoussova (1948), but they also have fewer whorls, typically $2\frac{1}{2}$-3, as against 3-4 in Russian material. The data in Table No.46 below, shows

that form ratio increases outwards from the earlier whorls to the latest, reaching 0.86 in the third whorl and, assuming that the increase in form ratio remains constant, 0.92 in the fourth whorl; a figure which is low in the range listed for E. sphaerica by Rauser-Chernoussova (1948). That range, however, is higher than it should be since it is based on imprecisely orientated sagittal sections. Furthermore, the endothyranopsids from the Upper Limestone Group normally have a greater number of chambers than E. crassa and they are, therefore, assigned to E. sphaerica.

Dimensions:

See Tables 45 and 46 below.

Depository:

Hunterian Museum of the University of Glasgow, P.474/1-14 on rock slices 1143/1-10, 1144/1-4 and 1146/2-3 from Castlecary Limestone, Westerwood Quarry, near Castlecary, Dumbartonshire, and P.475/1-5 on rock slices 311/1-10 from Plean Limestone, Beoch Bore, Beoch Farm, New Cumnock, Ayrshire.

Horizon and Facies:

Although species of Endothyranopsis are known to range throughout the Namurian of Russian Carboniferous, in the Upper Limestone Group Endothyranopsis sphaerica

has been recorded only from the Plean and Castlecary Limestones at the top of the group, and is not known from the lower limestones of the Upper Limestone Group, or, indeed, from any of the lowermost Namurian strata in Scotland.

TABLE 45

Whorl No.	Prol.	1	2	3
N	9	9	5	2
x		5.3	7.8	10.5
s		0.5	0.45	
ex		0.17	0.2	
V		10	6	
OR		5-6	7-8	10-11

DIAMETER

x	76	260	476	834
s	10	17	49	
cx	3	6	22	
V	13	6	10	
OR	60-86	206-301	404-533	722-946

TABLE 46

FORM RATIO

Whorl No.		1	1½	2	2½	3
	N	5	5	5	5	3
	x	0.776	0.81	0.846	0.83	0.863
	s	0.058	0.025	0.039	0.054	0.035
	ex	0.026	0.011	0.018	0.024	0.02
	V	8	3	5	7	4
	OR	0.72-0.86	0.78-0.84	0.80-0.89	0.78-0.91	0.82-0.88

TEXT - FIGURE 8.

A chart illustrating the phylogeny of the family Endothyridae, the distribution of its sub-families and some of its important genera in the Lower and Middle Carboniferous.

DEVONIAN
LOWER
CARBONIFEROUS
MIDDLE
FAMENIAN
TOURNAISIAN
VISEAN
NAMURIAN
WESTPHALIAN
QUASIENDOTHYRIDAE
TOURNAYELLIDAE
Mediocris
Mikhailovella
Endothyra
Globoendothyra
BRADYININAE
Endothranella
Novella
Endostaffella
Chernousovella
Millerella
Paramillerella
Pseudostaffella
Vissarionovella
Pseudoendothyra
ENDOTHYRIDAE
ENDOTHYRINAE
OZAWAINELLINAE
STAFFELLIDAE

STRATIGRAPHIC DISTRIBUTION.

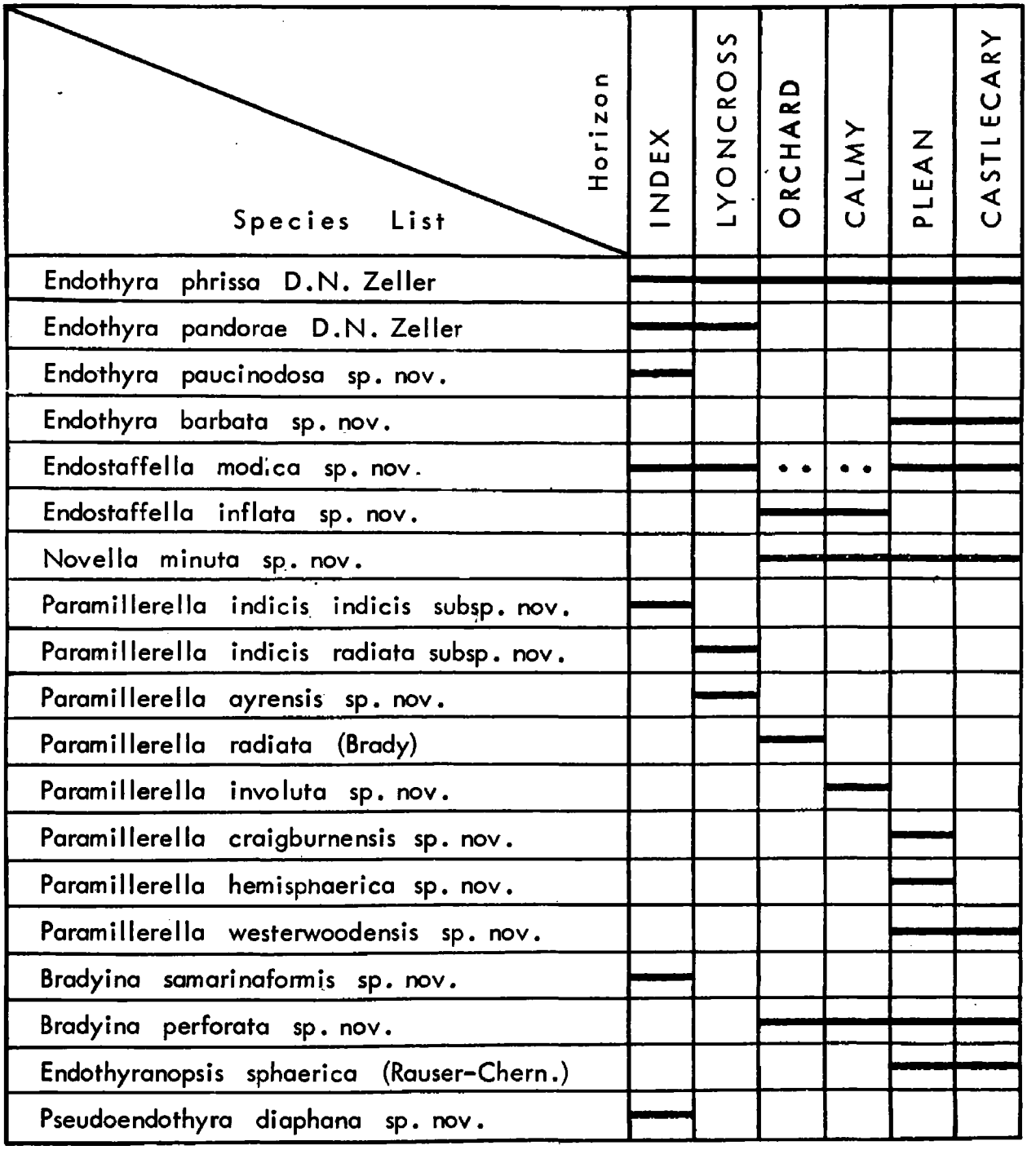
The phylogenetic and familial relationships of Endothyra, Paramillerella and the associated genera and subgenera, discussed herein, are summarised in Text fig.8. This chart indicates the range and relative abundance of the genera in Lower and Middle Carboniferous, based on their world wide occurrence as recorded in the literature.

The distribution of the species described above is summarised in Text fig.9, but, in this instance the information relates entirely to their occurrence in the Upper Limestone Group of the Scottish Carboniferous.

TEXT - FIGURE 9.

A chart showing the distribution of endothyrid species in the limestone horizons of the Upper Limestone Group.

RANGE OF ENDOTHYRID SPECIES WITHIN THE UPPER LIMESTONE GROUP



EXPLANATION OF PLATE 3.

All Figures X200.

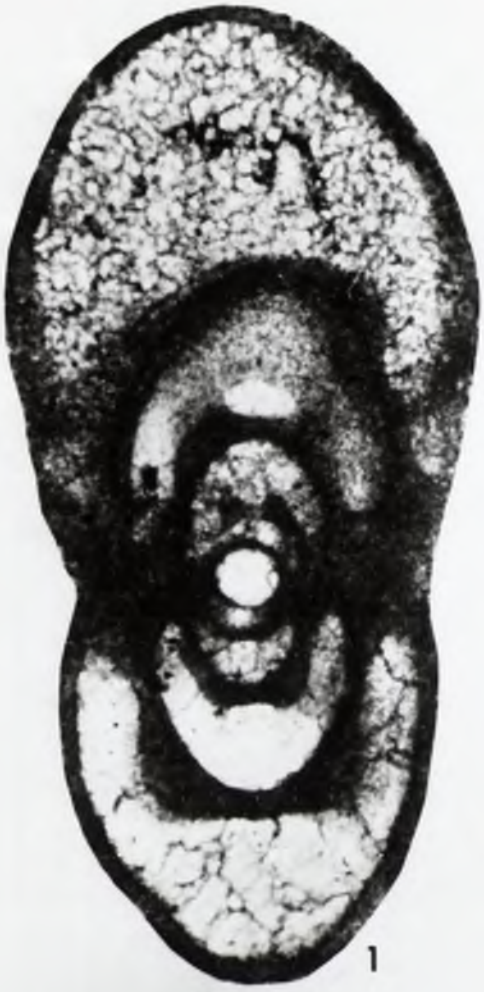
1. Paramillerella ayrensis sp. nov., Lyoncross Limestone, Craigburn, P.472/117:
Note the dark primary wall which is homogeneous, and largely without distinguishable granularity. It consists of a single layer which may have a discontinuous dark fringe on both inner and outer surfaces, resulting in part from optical effect of the continuous marginal interface, and in part from slight iron enrichment. Slightly more granular and lighter secondary deposits form platform-like chomata.

2,3. Paramillerella westerwoodensis sp. nov., Castlecary Limestone, Westerwood Quarry, P.471/41 and 39:

2. Recrystallised specimen showing the appearance of granularity in the wall, and iron enrich-:ment producing a dark band between the protheca and epitheca suggesting a tectum.
3. More severely recrystallised specimen showing the outer whorl merged peripherally with the matrix and the inner whorls with marked granularity. Iron enrichment forms

a prominent dark 'tectum' between protheca and epitheca. (cf. Plate 4, fig.2).

4. Endothyra pandorae (D.N. Zeller) Lyoncross Limestone, Garpel Water, P.438/3: horizontal axial section of a specimen in a host sediment showing marked iron enrichment: note the prominent limonite stain coating the interiors of the chambers and forming a dark inner layer ('lower tectoria') and a more discontinuous outer layer ('tectum'). (cf. Plate 5).



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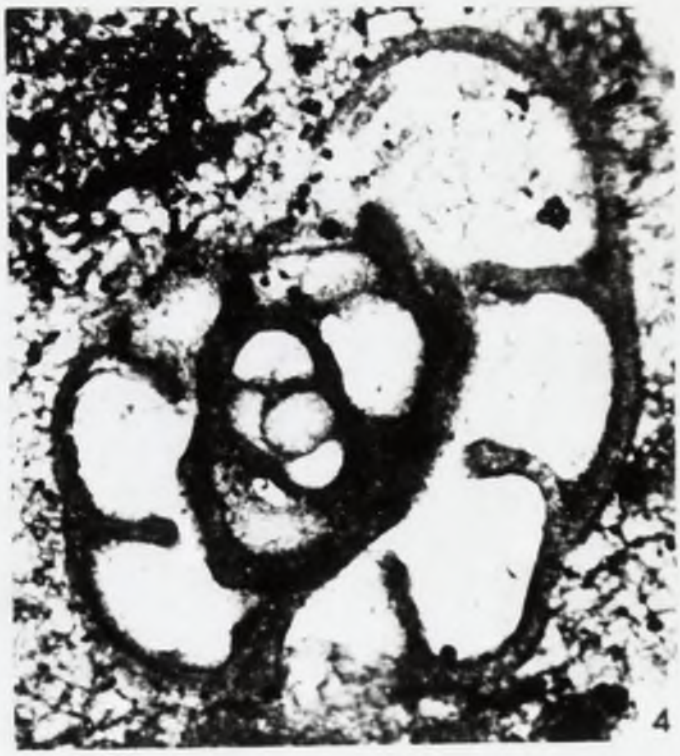

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EXPLANATION OF PLATE 4.

1. Bradyina cf. perforata sp.nov. Castlecary Limestone, Joppa, P.477: parallel sagittal section X100. A pyrite pseudomorph in a coarse crystalline dolomite in which much of the original fabric of the limestone has been destroyed by grain growth during replacement. Note the delicacy of the dusty pyrite replica within the mozaic of coarse crystals.

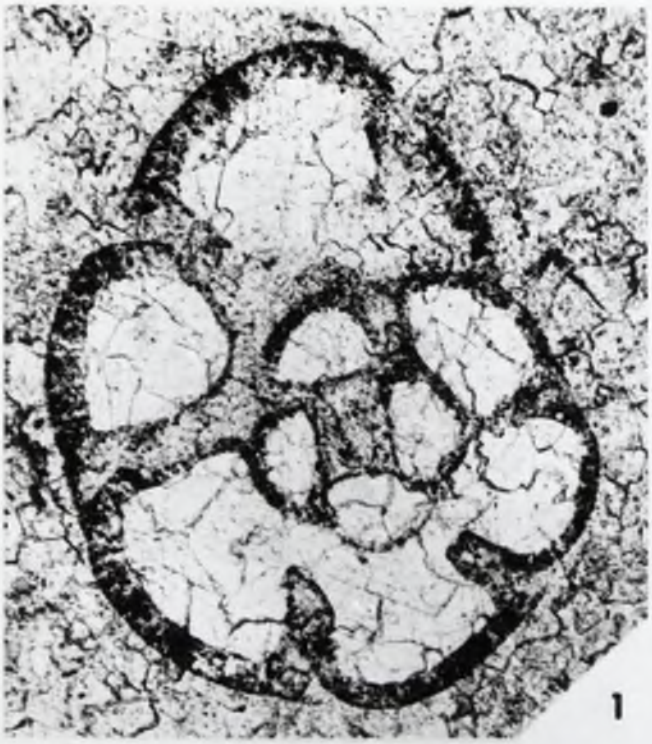
2. Paramillerella westerwoodensis sp.nov. Castlecary Limestone, Joppa, P.478; axial section X200. A strongly recrystallised specimen on the point of disappearance. Note coarseness of the crystals in the wall and the manner in which they merge with the matrix except where the zone of iron enrich-:ment picks out the boundaries. The recognition of the form of the test is dependant on the contrast between the grain size of the wall and the drusy calcite infilling of the test. (cf. Plate 3, figs.2-3).

3. Endothyra sp. Castlecary Limestone, Joppa, P.479/1; oblique section X200. Note the

PLATE 4. - cont.

manner in which the recrystallised wall merges with the matrix and the form of the test is preserved only by the drusy calcite infilling of the chambers which is more resistant to recrystallisation and so provides a marked contrast in grain size.

4. Endothyra sp. Castlecary Limestone, Joppa, P.479/2; oblique section X200. A contrasting mode of preservation in which the wall is replaced by coarse grained clear dolomite, but remains visible against the fine grained, heavily pyritised, infilling of the chambers.



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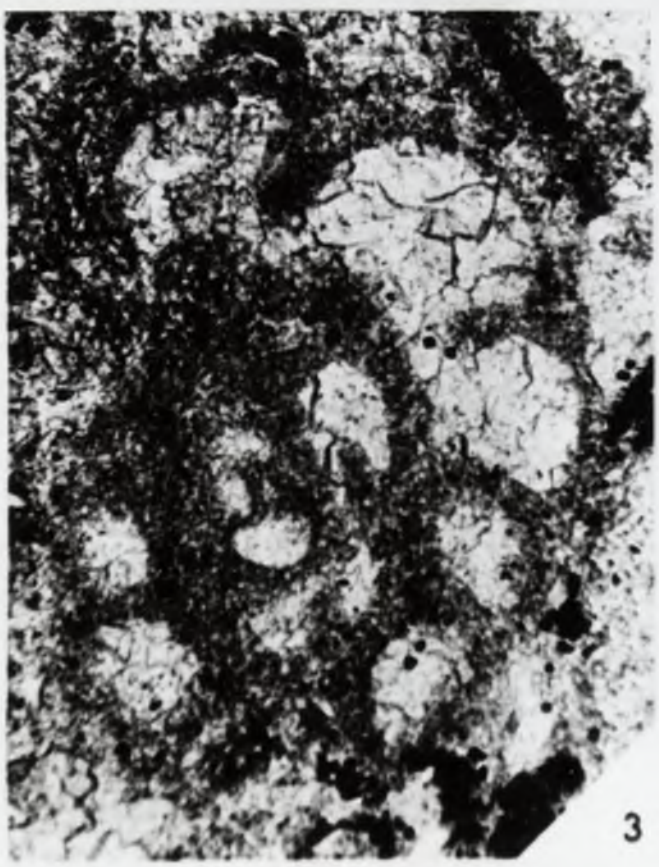

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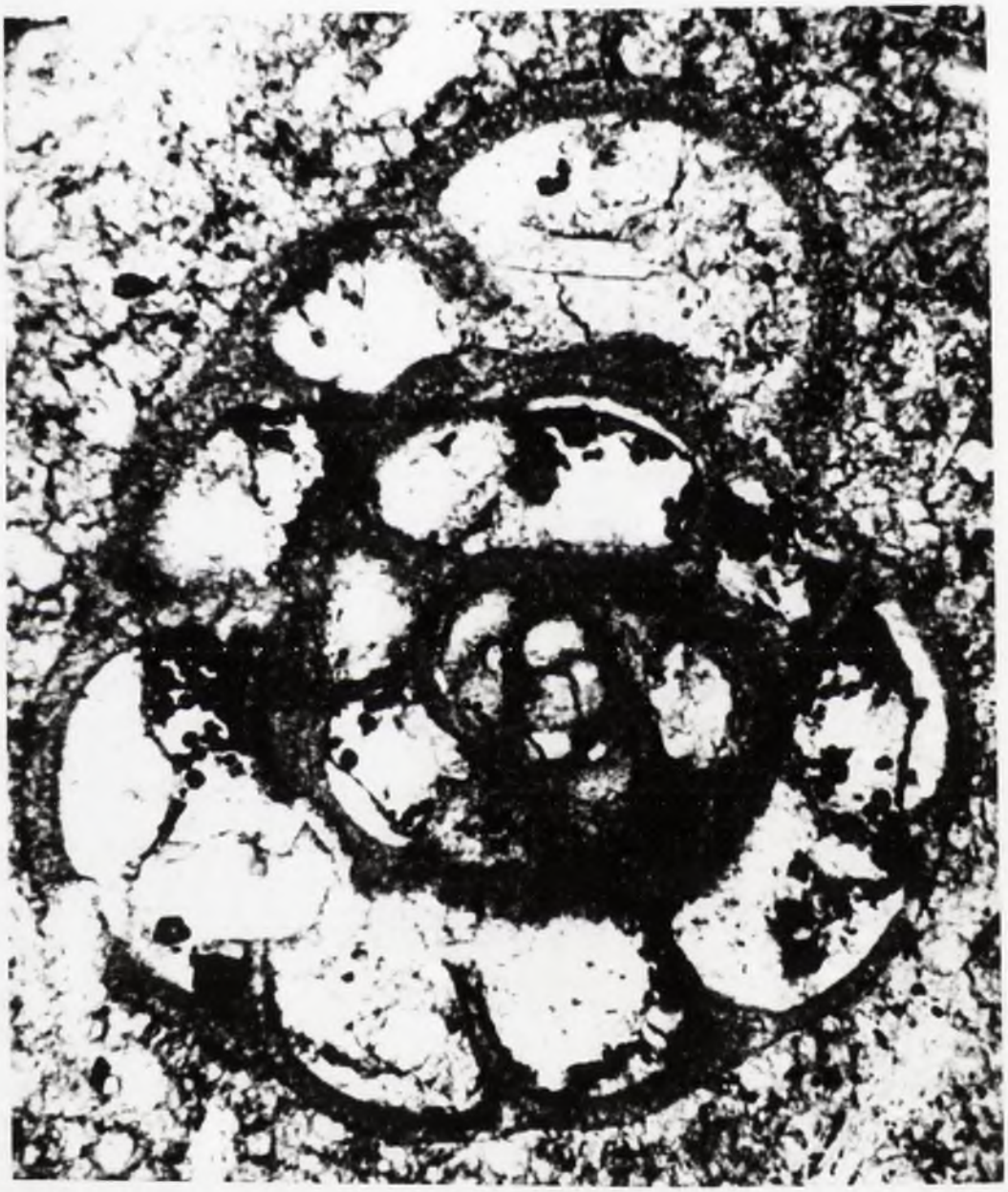
EXPLANATION OF PLATE 5.

1. Endothyra pandorae (D.N. Zeller), Lyoncross Limestone, Polbraith Burn, Killoch, Galston, P.480; oblique horizontal axial section X200. A recrystallised specimen in a host sediment showing extensive iron enrichment. Note the clusters of Pyritosphaera filling parts of the chambers. A dark selvage of limonitic staining occurs along the inner and outer margins of the wall, in the intercameral suture, and between the protheca and epitheca. At a number of points in the wall, dark transverse structures suggest iron ore filled pores.



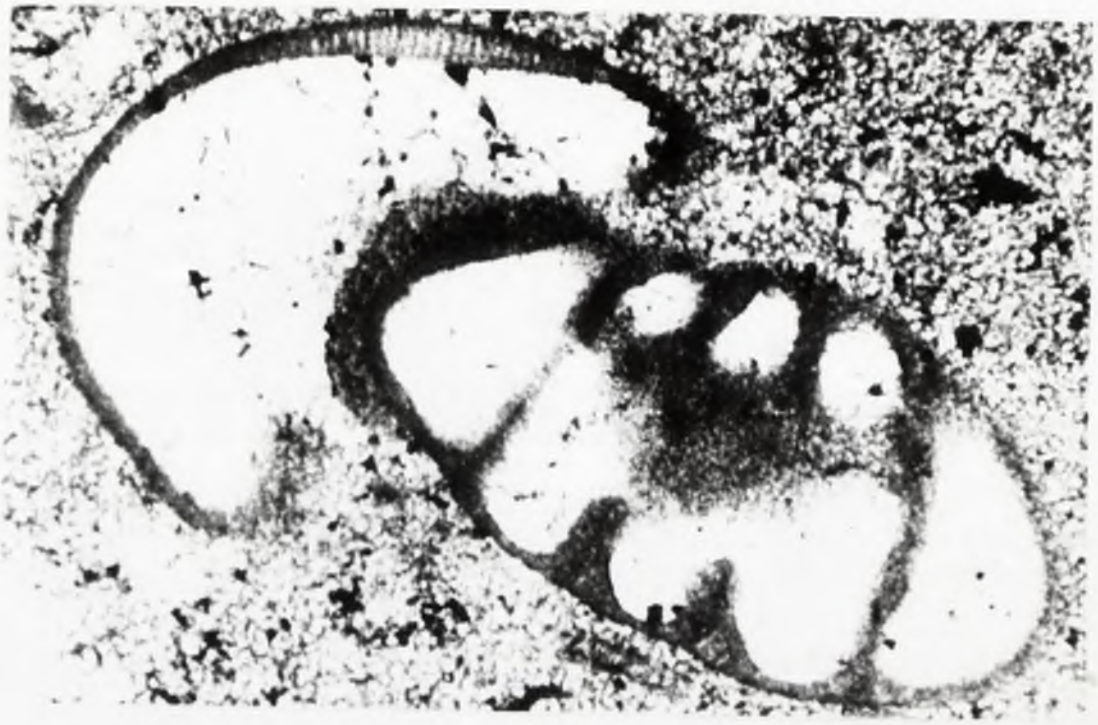
EXPLANATION OF PLATE 6.

1. *Paramillerella* sp. Lyoncross Limestone, Lugton Water, Montgreenan Bridge, P.481; oblique section X200. Although the coarsely alveolar texture and thickness of the wall of this specimen is exceptional its importance lies basically in the fact that the structure can be traced laterally into the normal wall and, therefore, suggests that this is its normal underlying structure.

2,3. *Paramillerella* sp. Lyoncross Limestone, Rye Water, West of Drakemire, Dalry, P.482;

2. parallel axial section X100.

3. the same specimen X200, Strong iron enrichment of the host sediment has lead to staining of the specimen bringing out the presence of transverse pores or alveolar structure in the protheca of the final half whorl.



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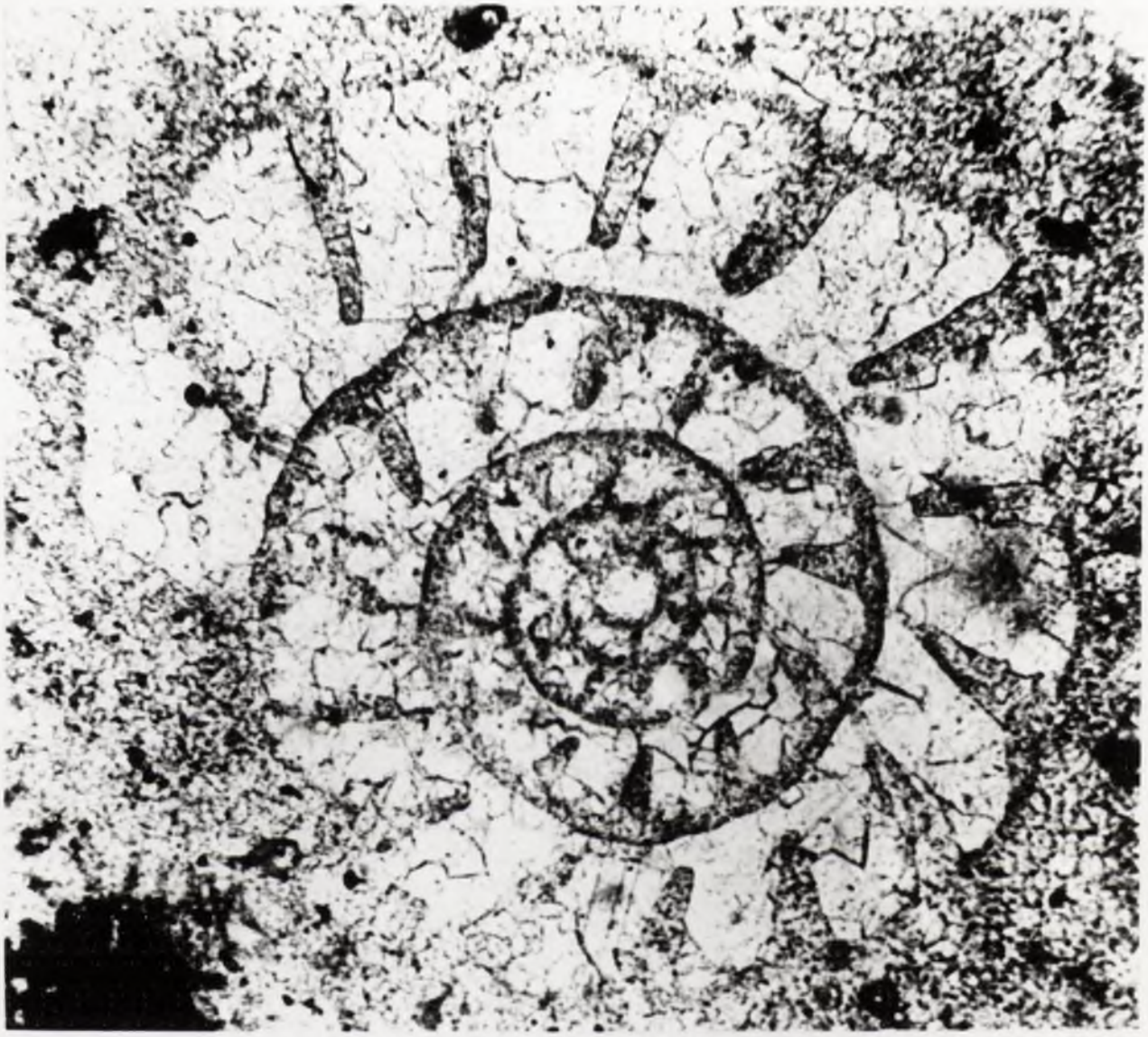
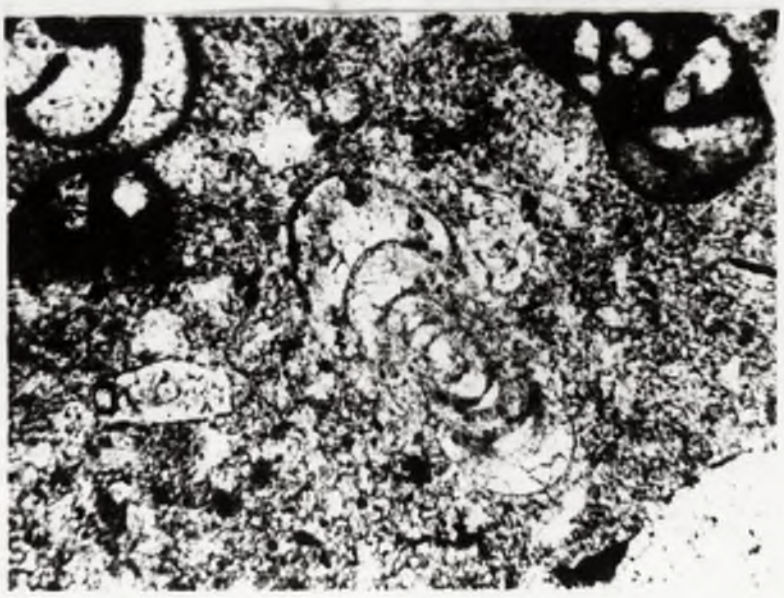
EXPLANATION OF PLATE 7.

Upper: Pseudoendothyra diaphana sp. nov. Index Limestone, Kennox Water, P.483/1; sagittal section X200. Note that the wall is translucent, coarsely granular, and the manner in which the outer margin of the outer wall merges with, and is indistinguish-:able from, the matrix, while the inner margin remains sharp against the coarse drusy infill-:ing of the test.

Lower: Pseudoendothyra diaphana sp. nov. Index Limestone, Poniel Water, P.461/6; axial section X100. A specimen showing typical ghostly translucent appearance. The outline of the test is preserved largely by the semi-:circular areas of drusy calcite filling the chambers, providing a complete contrast to the preservation in adjacent fragments of Endothyra.





EXPLANATION OF PLATE 8.

All figures X100 unless stated otherwise.

1. Paramillerella sp. Shale over Orchard Limestone, River Avon, Strutherhill, P.467/8; sagittal section showing complete reversal of coiling after first whorl. (cf. Plate 19, fig.3). The test is infilled by finely granular phosphate.

2. Paramillerella sp. Lyoncross Limestone, Overlee, Clarkston, P. 566 ; axial section showing aberrent coiling with an abrupt change in the direction of rotation.

3. Paramillerella sp. Shale over Orchard Limestone, River Avon, Strutherhill, P.467/9; sagittal section under X-nicols showing first two whorls filled by calcite, the remainder by calcium phosphate.

4. Paramillerella hemisphaerica sp. nov. Plean Limestone, Beoch Bore, P.484; small cluster of juvenile individuals X75. Note the manner in which the tests are fused together and resorbed within the cluster so that there is a mutual interconnection.

PLATE 8. - cont.

5. Plectogyra phrissa (D.N. Zeller), Shale over Orchard Limestone, River Avone, Strutherhill, P.432/5; horizontal axial section under X-nicols, showing test infilled by finely granular calcium phosphate.

6. Paramillerella craigburnensis sp. nov. Plean Limestone, Craigburn, Uddington, P.469/98; sagittal section under X-nicols, showing normal infilling drusy calcite.

7. Paramillerella cf. westerwoodensis, sp. nov. Castlecary Limestone, Westerwood Quarry, P.485; fused and internally resorbed cluster of juvenile individuals.

8-10. Lugtonia elongata, Cummings.

8. longitudinal section showing clear finely granular wall, chambers infilled largely by pyrite, X50.

9. the same specimen in X-nicols showing wall of finely granular calcium phosphate. Shales over Orchard Limestone, Poniel Water, P.486.

PLATE 8. - cont.

8-10. 10. longitudinal section of two chambers showing test wall composed of finely granular phosphate and chambers infilled by similar material. X-nicols; Shales over Orchard Limestone, River Avon, Strutherhill, P.487.

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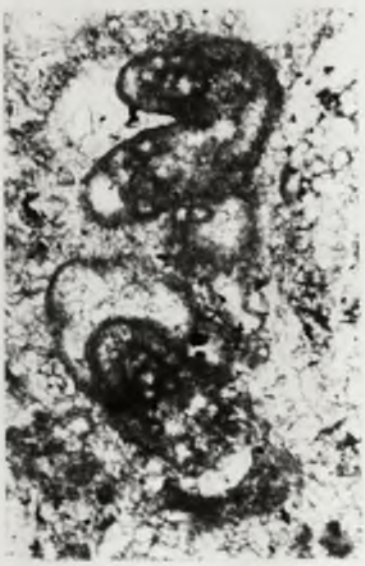

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EXPLANATION OF PLATE 9.

All figures X100 unless stated otherwise.

1-6,9. *Endothyra phrissa* (D.N. Zeller).

1. horizontal axial section, P.432/2.
2. horizontal axial section, P.432/3.
3. vertical axial section, P.432/4.

All from shales over Orchard Limestone, River Avon, Strutherhill.

4. oblique section, P.489; Index Limestone, Hullerhist Quarry.
5. horizontal axial section, P.490; Lyoncross Limestone, Whitecraigs, Renfrewshire.
6. oblique section, P.491; Lyoncross Limestone, Craigburn, Uddington.
9. horizontal axial section, P.492; Castlecary Limestone, Bowdenhill Quarry & Mine.

7-8, 10-13. *Endothyra barbata* sp. nov.

7. horizontal axial section, HOLOTYPE P.433/1;
8. parallel vertical axial section, P.433/2;

Both from Plean Limestone, Craigburn, Uddington.

10. vertical axial section, P.493/1.
11. horizontal axial section, P.493/2.
12. transverse section, P.493/3.
13. oblique section, P.493/4.

All from Castlecary Limestone, Westerwood Quarry.


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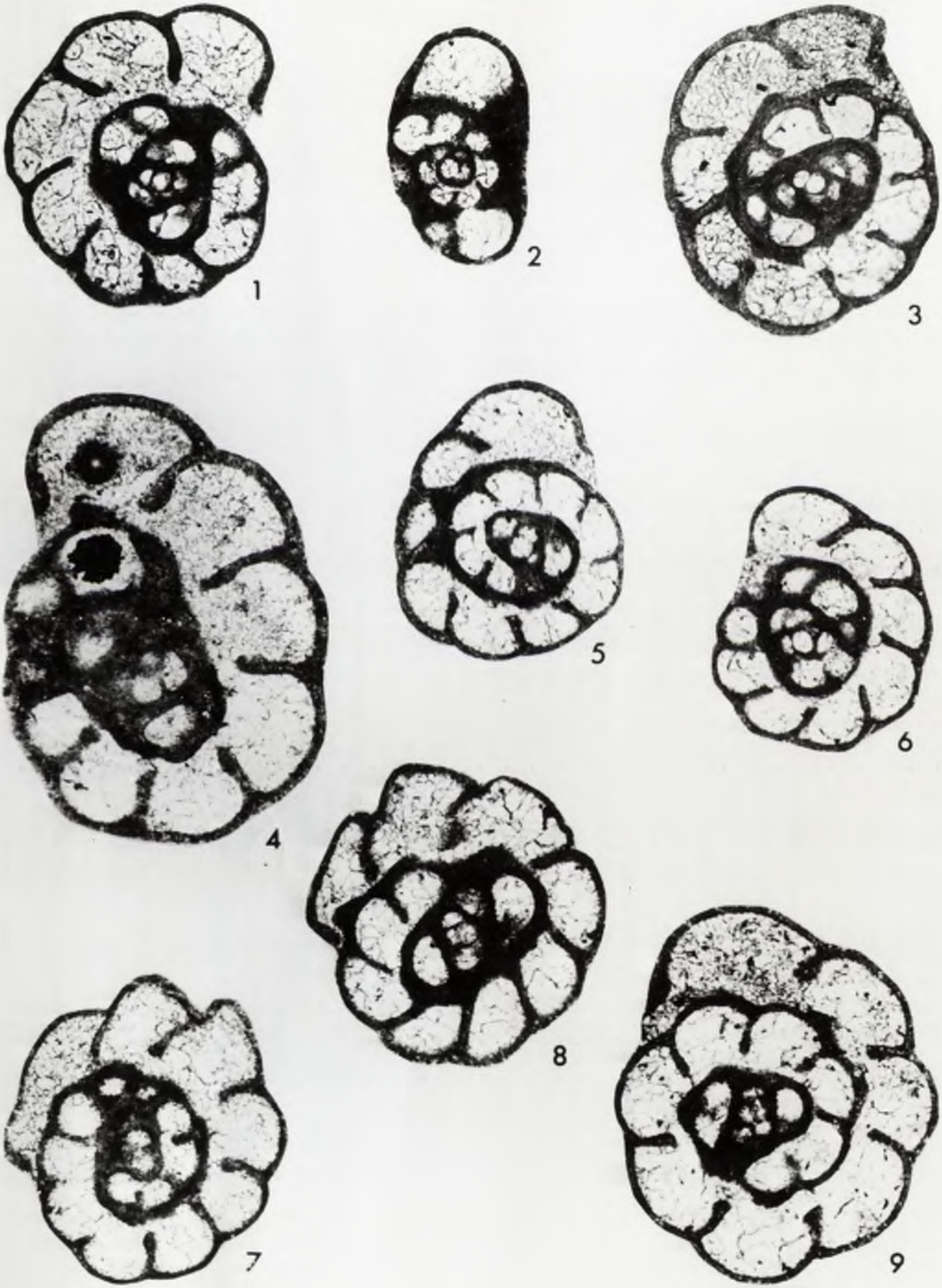
EXPLANATION OF PLATE 10.

All figures X100 unless stated otherwise.

1-8. Endothyra pandorae (D.N. Zeller).

1. horizontal axial section, P.436/1; Lyoncross Limestone, Overlee, Clarkston.
2. vertical axial section, P.437/2; Index Limestone, Poniel Water, Coalburn.
3. horizontal axial section, P.438/1; Lyoncross Limestone, Craigburn, Uddington.
4. parallel horizontal axial section, P.439; Index Limestone, Kennox Water.
5. oblique section showing thick secondary deposits in lateral part of the chamber P.436/2; and,
6. horizontal axial section P.436/3; both from Lyoncross Limestone, Overlee, Clarkston.
7. horizontal axial section showing collapsed crushed final chambers, P.494; and
8. horizontal axial section showing collapsed crushed final chambers, P.436/4; both from Lyoncross Limestone, Overlee, Clarkston.

9. Endothyra paucinodosa sp. nov.
Horizontal axial section, HOLOTYPE P.434; Index Limestone, Kennox Water.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EXPLANATION OF PLATE 11.

All figures X100 unless stated otherwise.

1-14. *Endostaffella modica* sp.nov.

1. horizontal axial section, P.444/1.
2. vertical axial section, P.444/2.
3. horizontal axial section, HOLOTYPE P.444/3.
4. horizontal axial section, P.444/4.
5. transverse section, P.444/6.
6. oblique section showing asymmetry of final whorls, P.444/10.

All from Index Limestone, Poniel Water, Coalburn.

7. horizontal axial section showing large proloculum and near planispiral coiling, P.445/2.
8. horizontal axial section showing strong axial rotation accentuated by plane of section lying oblique to the final whorl, P.445/5.
9. vertical axial section showing that final whorl is not planispiral as is indicated by the section meeting the septa in the final whorl (upper left and lower right), P.455/6.

All from Lyoncross Limestone, Whitecraigs.

PLATE 11. - cont.

10. vertical axial section, P.446/4.

11. vertical axial section, P.446/6.

12. horizontal axial section, P.446/8.

13. horizontal axial section, P.446/9.

14. transverse section, P.446/10.

All from Lyoncross Limestone, Overlee, Clarkston.

15-20. Endostaffella inflata sp. nov.

15. horizontal axial section, P.448/1.

16. horizontal axial section showing rapid expansion of the spiral and strongly inflated chernyshinellid form of the chambers in last whorl, HOLOTYPE P.448/3.

17. vertical axial section, P.448/4.

All from Orchard Limestone, Poniel Water, Coalburn.

18. horizontal axial section, P.449/1.

19. horizontal axial section, P.449/2.

Both from Orchard Limestone, Garpel Water, Muirkirk.

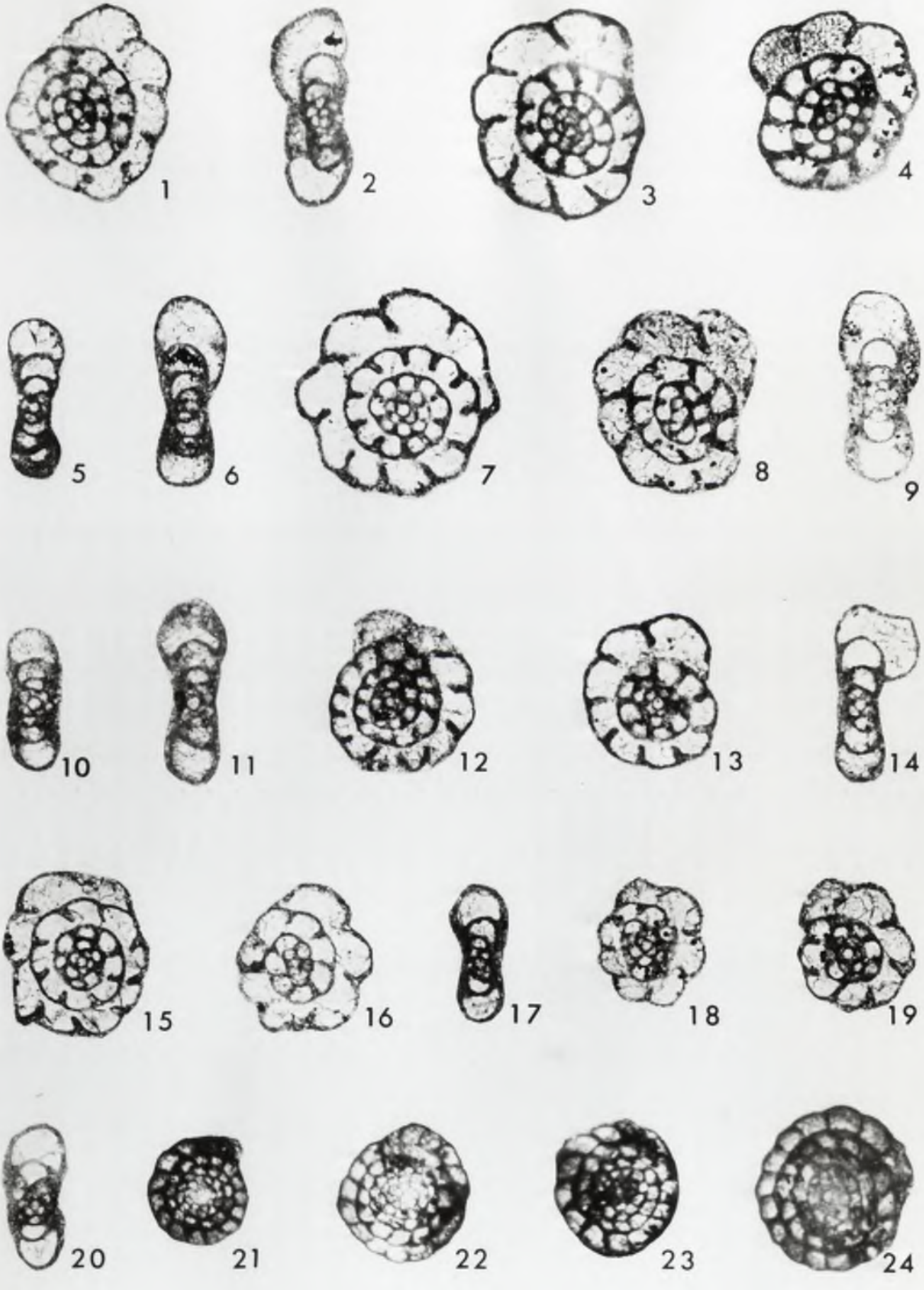
20. vertical axial section, P.495; Orchard Limestone, Lugton Water, Montgreenan.

21-24. Novella minuta sp. nov. from shale over Orchard Limestone, River Avon, Strutherhill.

PLATE 11. - cont.

21-24 complete specimens rendered transparent in clove oil, seen in transmitted light as sagittal sections, P.440/1-4:

24. HOLOTYPE P.440/4, see also Plate 31, fig.4.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EXPLANATION OF PLATE 12.

1-9. *Novella minuta* sp.nov.

1. slightly oblique sagittal section, P.441/2.
2. sagittal section, P.441/3.
3. parallel axial section, P.441/5.

All from Orchard Limestone, Poniel Water, Coalburn.

4. oblique sagittal section showing chambers infilled by pyrite and wall replaced by dolomite, P.442/1.
5. slightly oblique sagittal section, P.442/3.

Both from thin limestone bands over Calmy Limestone, River Nethan, near Auchlochan House.

6. sagittal section, P.496; Calmy Limestone, Castlecary Castle.
7. axial section, P.443; Calmy Limestone, Monkcastle Burn, Dalry.
8. axial section P.497/1.
9. slightly oblique sagittal section.

Both from Castlecary Limestone, Westerwood Quarry.

PLATE 12. - cont.

10-17. Paramillerella indicis indicis subsp. nov.

10. axial section, P.460/1.

11. axial section, P.460/10.

12. sagittal section showing quadrate, slightly inflated, chambers, P.460/22.

13. oblique section showing inflated chambers and character of secondary deposits in lateral part of chambers, P.460/21.

14. sagittal section showing inflated quadrate chambers and thick basal layer of epitheca HOLOTYPE P.460/10.

15. axial section, P.460/14.

16. axial section, P.460/141.

All from Index Limestone, Poniel Water, Coalburn.

17. axial section showing very large proloculum P.462; Index Limestone, Auldhouse Burn, Muirkirk.

18-20. Paramillerella indicis subradiata subsp. nov.

18. axial section, P.462/98.

19. sagittal section showing quadrate inflated chambers, large proloculum, P.462/99.

20. axial section, P.462/100.

All from Lyoncross Limestone, Overlee, Clarkston.


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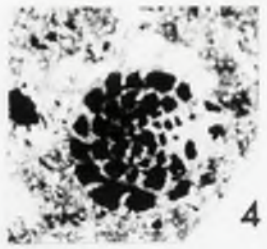
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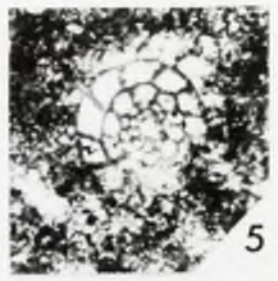
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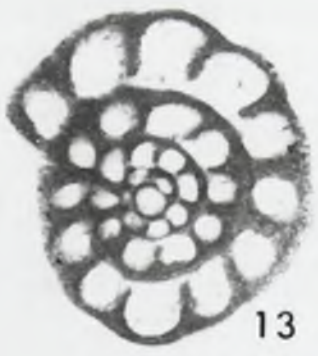
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EXPLANATION OF PLATE 13.

All figures X100.

1,2. *Paramillerella indicis subradiata* subsp. nov.

1. axial section showing oblique early coiling, P.462/101; Lyoncross Limestone, Overlee, Clarkston.
2. sagittal section showing weak inflation of chambers and quadrate form, P.463/138; Lyoncross Limestone, Whitecraigs, Renfrewshire.

3,4. *Paramillerella radiata* (Brady).

3. axial section showing compression of final whorl through compaction, the irregular loss of the outer wall of test, and oblique early whorls, PARATYPE ex slide P.353631; Brady Collection, B.M.N.H. (see Plate 19, figs.7,8).
4. sagittal section, very thick, PARATYPE P.31567 ex slide P.35361, Brady Collection B.M.N.H. Shales over Orchard Limestone, Gillfoot, Crossford.

5-12. *Paramillerella radiata* (Brady).

5. axial section showing the effects of compaction; note the compression of outer and inner whorls, P.467/1.

PLATE 13. - cont.

6. axial section showing heavy chomata, nearly planispiral with large proloculum, P.467/2.

7. sagittal section showing wedge-like pattern of septa, P.467/3.

8. sagittal section showing small proloculum, strongly asymmetrical coiling, P.467/4.

9. sagittal section showing wedge-like form of septa and apparent resorption of septa in part of test, P.467/5.

10. sagittal section showing rectangular shape of chambers, P.467/6.

11. axial section showing heavy secondary deposits and compression of outer whorls, P.467/7.

All above from shale over Orchard Limestone, River Avon, Strutherhill.

12. axial section showing some compression in sagittal plane, P.465/56; Orchard Limestone, Poniel Water, Coalburn.

13-14. Paramillerella involuta sp. nov.

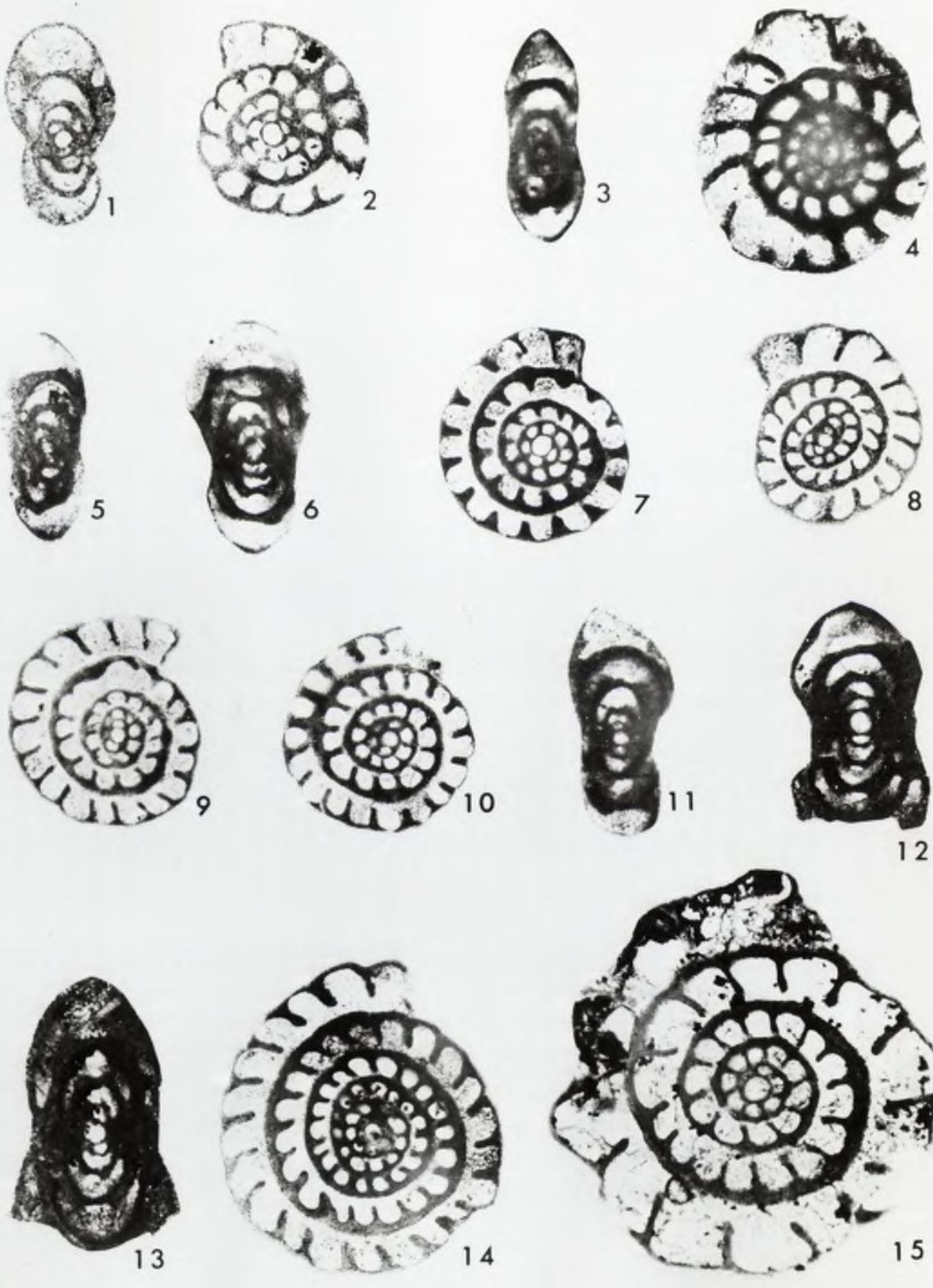
13. axial section P.468/80.

14. sagittal section,

From thin limestone over Calmy Limestone, Spireslack, Glenbuck.

PLATE 13. - cont.

15. Paramillerella ayrensis sp. nov.
Sagittal section showing crushing and collapse of chambers in outer whorl, P.498/1; from shale parting in Lyoncross Limestone, Craigburn, Uddington.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EXPLANATION OF PLATE 14.

All figures X100.

1-11. *Paramillerella ayrensis* sp. nov.

1. sagittal section showing some damage to chambers in final whorl, and aperture at base of final chamber, P.472/117; Lyoncross Limestone, Craigburn, Uddington.
2. parallel sagittal section showing rectangular chambers, P.449/1; Lyoncross Limestone, Kennox Water.
3. axial section with large proloculum, dark homogeneous primary wall and slight irregularity in coiling, P.500/1; Lyoncross Limestone, Lugton Water, Montgreenan.
4. axial section showing platform-like chomata, P.473/71; Lyoncross Limestone, Garpel Water, Muirkirk.
5. sagittal section, P.498/2;
6. sagittal section showing small proloculum with sharp deviation in coiling of first whorl, P.498/3;;

Both above from shale parting in Lyoncross Limestone, Craigburn, Uddington.

PLATE 14. - cont.

7. axial section showing first whorl almost in sagittal plane, P.472/119; Lyoncross Limestone, Garpel Water, Muirkirk.

8. axial section, P.472/118;

9. axial section, P.472/119;

11. axial section, P.472/120;

above from Lyoncross Limestone, Craigburn, Uddington.

10. sagittal section, P.498/4; shale parting in Lyoncross Limestone, Craigburn, Uddington.


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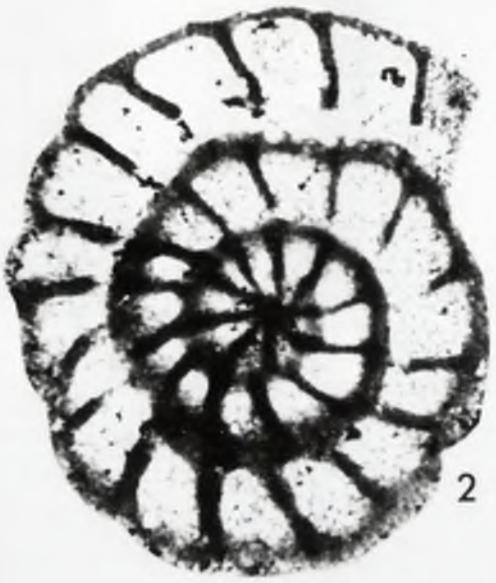
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EXPLANATION OF PLATE 15.

All figures X100.

1-6. Paramillerella ayrensis sp. nov. Lyoncross Limestone.

1. axial section, P.501; Rye Water, West of Drakemire, Dalry.
2. axial section, P.500/2; Lugton Water, West of Montgreenan Bridge.
3. sagittal section, P.472/121; Craigburn, Uddington.

4,6. axial sections, P.473/72 and 73; Garpel Water, Muirkirk.

5. sagittal section, P.499/2; Kennox Water.

7-14. Paramillerella westerwoodensis sp. nov. Castlecary Limestone, Westerwood Quarry.

7. axial section, P.471/41 (see Plate 3, fig.2).
8. axial section, P.471/39 (see Plate3, fig.3).
9. slightly oblique sagittal section, P.471/4.
10. axial section, P.471/43.
11. axial section, P.471/42.
12. axial section, P.471/38.

PLATE 15. - cont.

13. sagittal section showing arcuate long septa, numerous chambers and large proloculum, HOLOTYPE P.471/13.

14. axial section, P.471/37.


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EXPLANATION OF PLATE 16.

All figures X100.

1-5. *Paramillerella craigburnensis* sp. nov.

1. sagittal section with numerous rectangular chambers. Note thick basal layer epitheca, and aperture, HOLOTYPE P.469/72.
2. axial section showing thin, dark, protheca, more coarsely granular massive secondary deposits, forming prominent chomata, and strongly asymmetrical tunnel, P.469/27.
3. axial section, P.469/23.
4. sagittal section showing basal layer extending beyond final chamber, which is broken, P.469/98.
5. sagittal section, P.469/84.

All from Plean Limestone, Craigburn, Uddington.

6-9. *Paramillerella hemisphaerica* sp. nov.

6. axial section of juvenile showing prominent chomata, P.470/138.
7. axial section, P.470/139.
8. oblique sagittal section showing thick development of epitheca in lateral part of test, P.470/140.

PLATE 16. - cont.

9. axial section showing broadly rounded hemispherical periphery, prominent chomata, P.470/141.

All from Plean Limestone, Beoch Bore.


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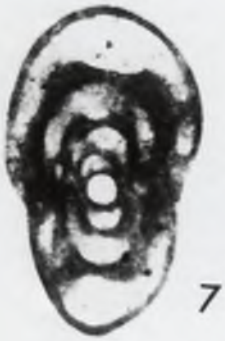
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EXPLANATION OF PLATE 17.

1-6. *Paramillerella hemisphaerica* sp. nov.

1. sagittal section showing numerous chambers, many irregularly formed, thick basal deposits, and crushed and collapsed final whorl, HOLOTYPE P.470/109.
2. axial section showing massive chomata, dark homogeneous protheca, damaged final whorl, P.470/54.
3. sagittal section, P.470/107.
4. parallel axial section of complete specimen showing basal aperture, P.470/142.
5. sagittal section with final whorl almost obliterated by recrystallisation, P.470/143.
6. axial section showing irregularity of tunnel path and prominent chomata, P.470/38.

All from Plean Limestone, Beoch Bore.

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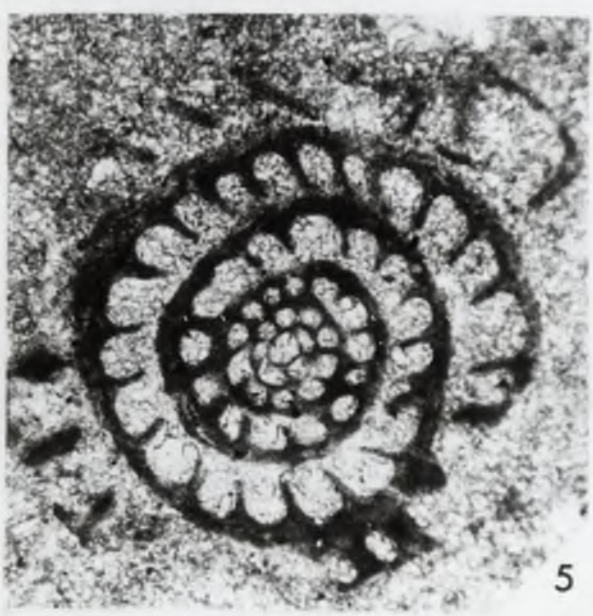

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EXPLANATION OF PLATE 18.

All figures X100.

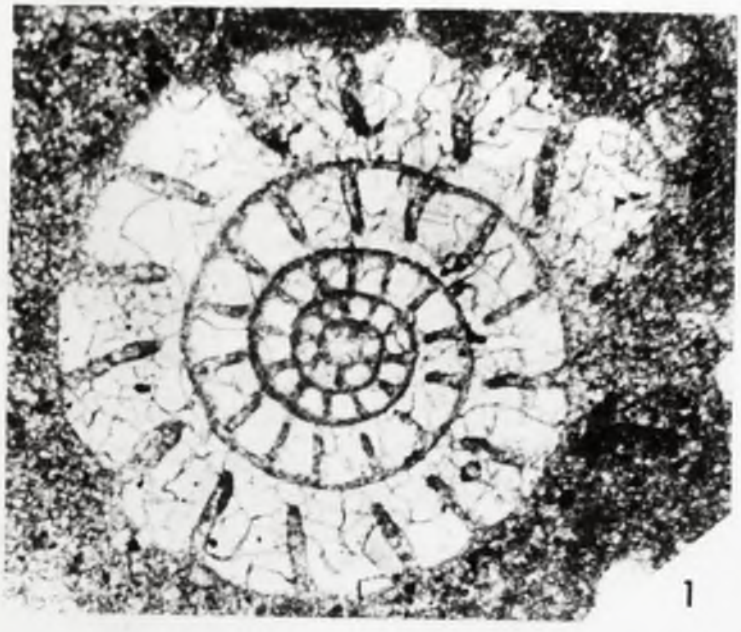
1-5. *Pseudoendothyra diaphana* sp. nov. Index Limestone.

1. sagittal section showing large rectangular chambers with long tapering wedge-like septa, HOLOTYPE P.461/3; Poniel Water, Coalburn.
2. axial section showing sparse secondary deposits thickening only base of septa adjacent to tunnel, P.483/2.
3. sagittal section showing typical recrystallised fabric, P.483/1.

Both from Kennox Water, Douglas.

4. oblique sagittal section showing recrystallisation of the wall adjacent to normally preserved fragment of *Endostaffella*, P.461/8.
5. axial section showing more rounded periphery of early whorls, P.461/6.

Both from Poniel Water, Coalburn.



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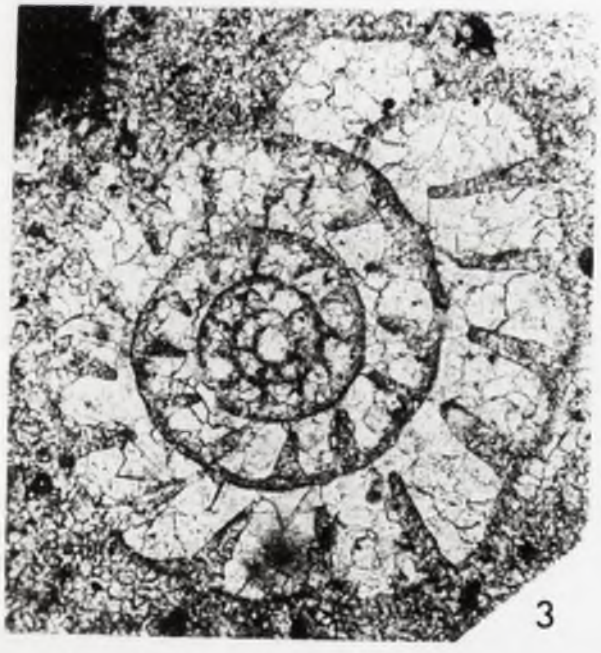

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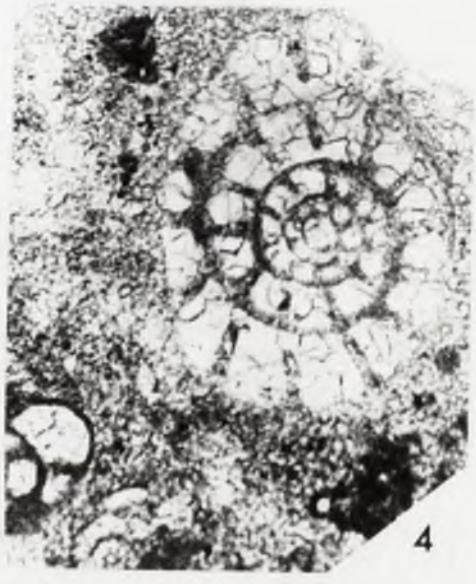

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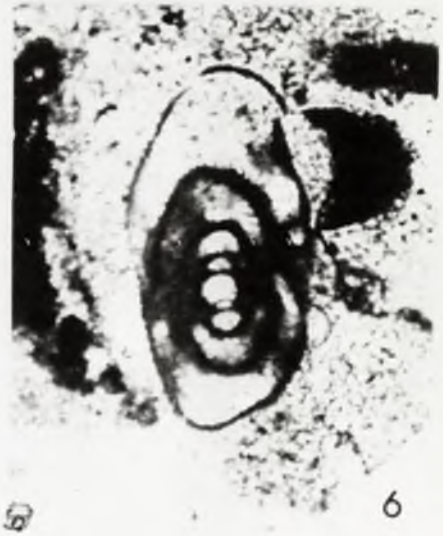

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EXPLANATION OF PLATE 19.

All figures X100.

1. Endothyra pandorae (D.N. Zeller).
horizontal axial section from limestone slice in reflected light, P.437/1; Index Limestone, Poniel Water, Coalburn.

2. Paramillerella westerwoodensis, sp. nov.
sagittal section showing long arcuate septa, P.471/11; Castlecary Limestone, Westerwood Quarry.

3. Paramillerella sp.
sagittal section revealing complete reversal of coiling after one and a half whorls, P.502; Lyoncross Limestone, Craigburn, Uddington.

4-6. Paramillerella ayrensis, sp. nov.

4. sagittal section showing rapidly expanding spiral, rectangular chambers. HOLOTYPE P.472/65; Lyoncross Limestone, Craigburn, Uddington.

5,6. apertural and lateral view of free specimen, P.498/5; shale partings in Lyoncross Limestone, Craigburn, Uddington.

PLATE 19. - cont.

7-10. *Paramillerella radiata* (Brady).

7-8. lateral and apertural views, B.M.N.H. P.35631 (see Plate 13, fig.3), Orchard Shale, Gillfoot, Crossford.

9-10 lateral views of specimens, P.467/10 and 467/11; from shale over Orchard Limestone, River Avon, Strutherhill.


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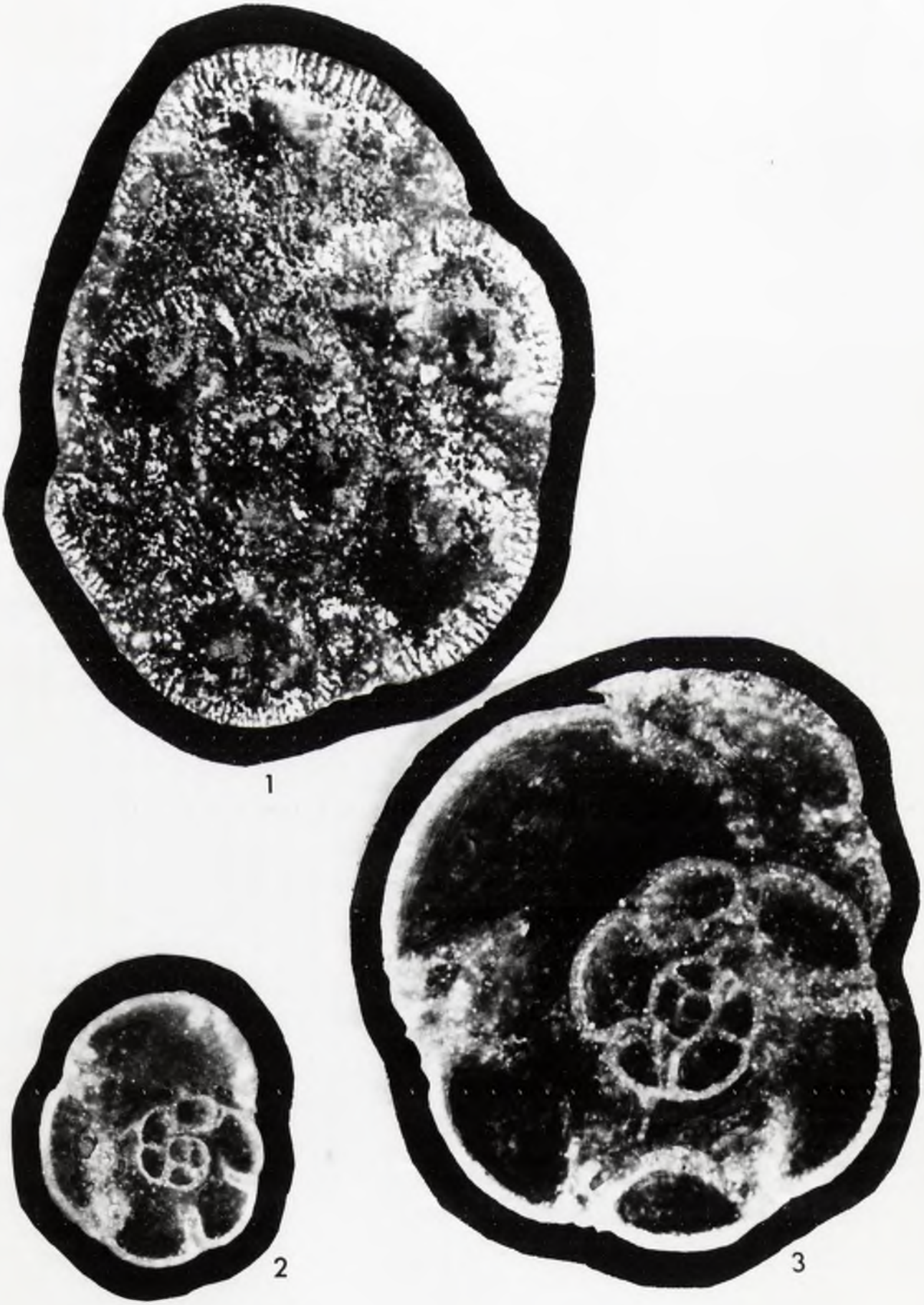
EXPLANATION OF PLATE 20.

1. *Bradyina perforata* sp. nov.
   sagittal section in reflected light and showing thick wall with alveoli infilled by pyrite, X50, HOLOTYPE P.451; Orchard Limestone, River Avon, Strutherhill.

2,3. *Bradyina samarinaformis* sp. nov.

2. sagittal section from limestone slice in reflected light showing slender wall rapidly expanding chambers, X25, P.450/6.

3. sagittal section showing thin wall, X50, HOLOTYPE P.450/17.



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EXPLANATION OF PLATE 21.

1-4. *Bradyina perforata* sp. nov.

1. parallel sagittal section showing coarsely alveolar wall, P.459/6.
2. oblique axial section, P.459/7.

Both from Castlecary Limestone, Westerwood Quarry.

3. axial section, P.455/2; from Orchard Limestone, Poniel Water, Coalburn.
4. sagittal section showing coarse alveolar wall, P.453; from Orchard Limestone, Garpel Water, Muirkirk.

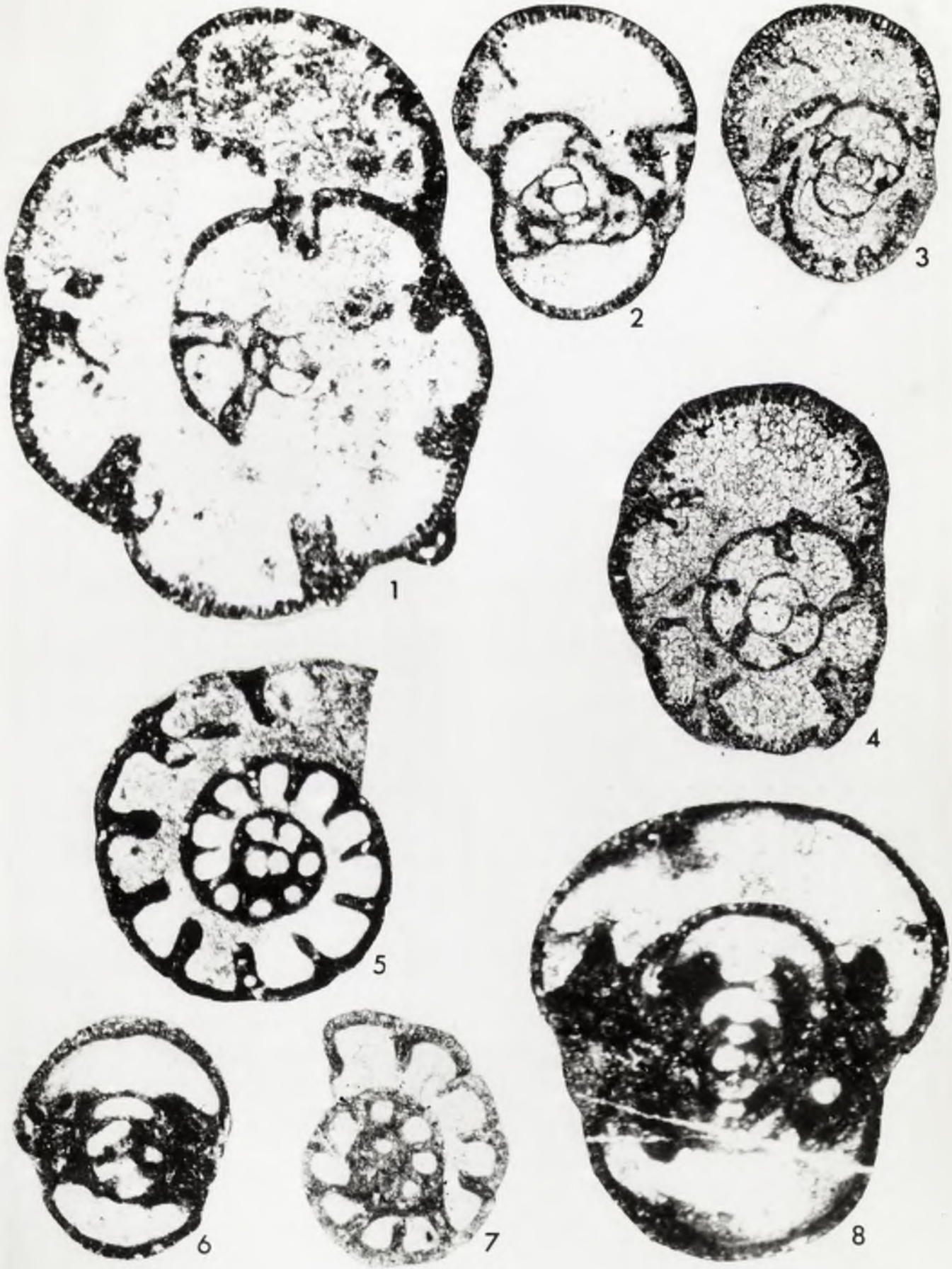
5-8. *Endothyranopsis sphaerica* (Rauser-Chernoussova, Beljaev & Reitlinger).

5. sagittal section showing irregularity in early coiling and thickening of the septal ends by epitheca, P.475/1;
8. axial section showing dense epitheca in lateral parts of chambers, P.475/4;

Both from Plean Limestone, Beoch Bore.

6. axial section showing irregularity of early coiling, P.475/15;
7. sagittal section showing pores in the wall, P.474/16;

Both from Castlecary Limestone, Westerwood Quarry.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FORAMINIFERA OF THE UPPER LIMESTONE GROUP OF THE SCOTTISH CARBONIFEROUS.

Volume 2.

A. N. Hutton.

C O N T E N T S.

VOLUME 2.

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TEXT FIGURES.

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TEXT FIGURES - VOLUME 2.

PLATES - VOLUME 2.

TABLES - VOLUME 2.

CHAPTER 4.

The structure of *Valvulina plicata* Brady, 1876 and its relationship to *Tetrataxis* and other Carboniferous foraminifers.

- oOo -

The structure of Valvulina plicata Brady, 1876 and its relationship to Tetrataxis and other Carboniferous foraminifers.

Although a small number of species of simple trochoid foraminifers have been described as free specimens from the Carboniferous (Brady, 1876, Cushman & Waters, 1927 and 1930, Warthin 1930, Bhatia & Singh 1959, and Conkin 1961) as yet they do not appear to have been figured or recognised in thin section. This would seem to be, in part, due to the genuine scarcity of species exhibiting this type of morphology, but it is not wholly attributable to this cause. Many records of trochoid species have been lost through confusion of their random sections with other genera. (Termier & Termier, 1950, p.35,36, Plate 1, figs.23-29; Davis, 1951, Plate 2, fig.7; Cummings, 1961, Plate IV, etc.).

Recent investigations of the simple trochoid foraminifers of the Carboniferous reveals that, although they exhibit an almost complete identity of form, they cannot be assigned to a single genus, for at least two fundamentally different wall structures are to be found within this group. Re-examination of Brady's type material shows that Valvulina plicata Brady has a wall structure which demonstrates its affinities with the

family Tetrataxidae, and, consequently, this species is proposed as the type of a new genus Helicospirina. A review of the morphology of this genus in random sections reveals that its characters have been confused with various other genera, notably Tetrataxis, Globivalvulina, and Howchinia.

This study shows the necessity for a more careful analysis of the morphology of Tetrataxis and discloses the inadequacies of much of the modern systematic treatment of this genus, as has been discussed by Vasicek & Ruzicka (1957 p.353).

For similar reasons Globivalvulina bulloides (Brady) is redescribed with thin sections of type material illustrating its internal structure, and the genus is recorded for the first time from the Scottish Carboniferous.

Modern research on Carboniferous agglutinate foraminifers has tended to suggest that most species possessed a primary siliceous cement (Ireland, 1956 p.840, Gutschick & Treckman 1959, pp.229-250 and Conkin 1961, pp.135-370). In particular, Conkin (1961 pp.234-236), has discussed the problems of wall structure in Palaeozoic agglutinate foraminifers at some length, but without reaching any conclusive assessment of its taxonomic significance. Nevertheless, it is clear that he regards the nature of the cement

a fundamental character, and he argues that isomorphous foraminifers can only be regarded as distinct genera if they differ in this character. The discovery of trochoid agglutinate forms, with an undoubtedly calcareous cement, in the Upper Limestone Group of the Scottish Carboniferous, therefore poses questions of fundamental taxonomic importance among Palaeozoic agglutinate foraminifers. It is considered, however, that these problems are best reviewed in the light of Hedley's (1963) work on recent arenaceous foraminifers and the view expressed by Cummings (1955 & 1956) that the foraminiferal wall, as it reflects the dual metabolic functions of secretion and selection, provides a reliable basis for morphological classification.

MORPHOLOGY.

In Brady's (1876) description of Valvulina plicata he commented on its close relationship with Valvulina palaeotrochus (Ehrenberg) (Tetrataxis) and suggested that the species differed only in the form and arrange-:ment of the chambers in the former species. This statement has been substantially confirmed through examination of type material from Brady's collections, and material occuring within the Upper Limestone Group, which shows that, although V. plicata is effectively an isomorph of Trochammina, it has a wall structure which demonstrates conclusively its affinities with tetrataxids.

The wall in the early stages is granular calcareous and, although typically at this stage, it lacks a 'fibrous' layer, the rather coarse granules in the wall and its light appearance are closely comparable with the granular layer of a tetrataxid. (Plate 22, figs.1-4). Moreover, the appearance in the later stages of some specimens of a thin 'fibrous' element provides confirm-:ation of this observation. (Plate 22, fig.2).

Warthin (1930 p.25), regarded V. plicata as a species of Tetrataxis, however, although both Tetrataxis and Helicospirina are trochoid foraminifers exhibiting a common wall structure, they differ considerably in

TEXT - FIG.10.

Helicospirina plicata gen. et sp. nov.

A Sagittal section; showing circular cross section of umbilical wall and aperture adjoining umbilicus.

B Lateral view; observing D laterally from a position at B.

C Oblique section; in plane shown in B. Note superficial resemblance to Globivalvulina. This section distinguish-:able by means of the section through the umbilicus and the lack of true biseriality.

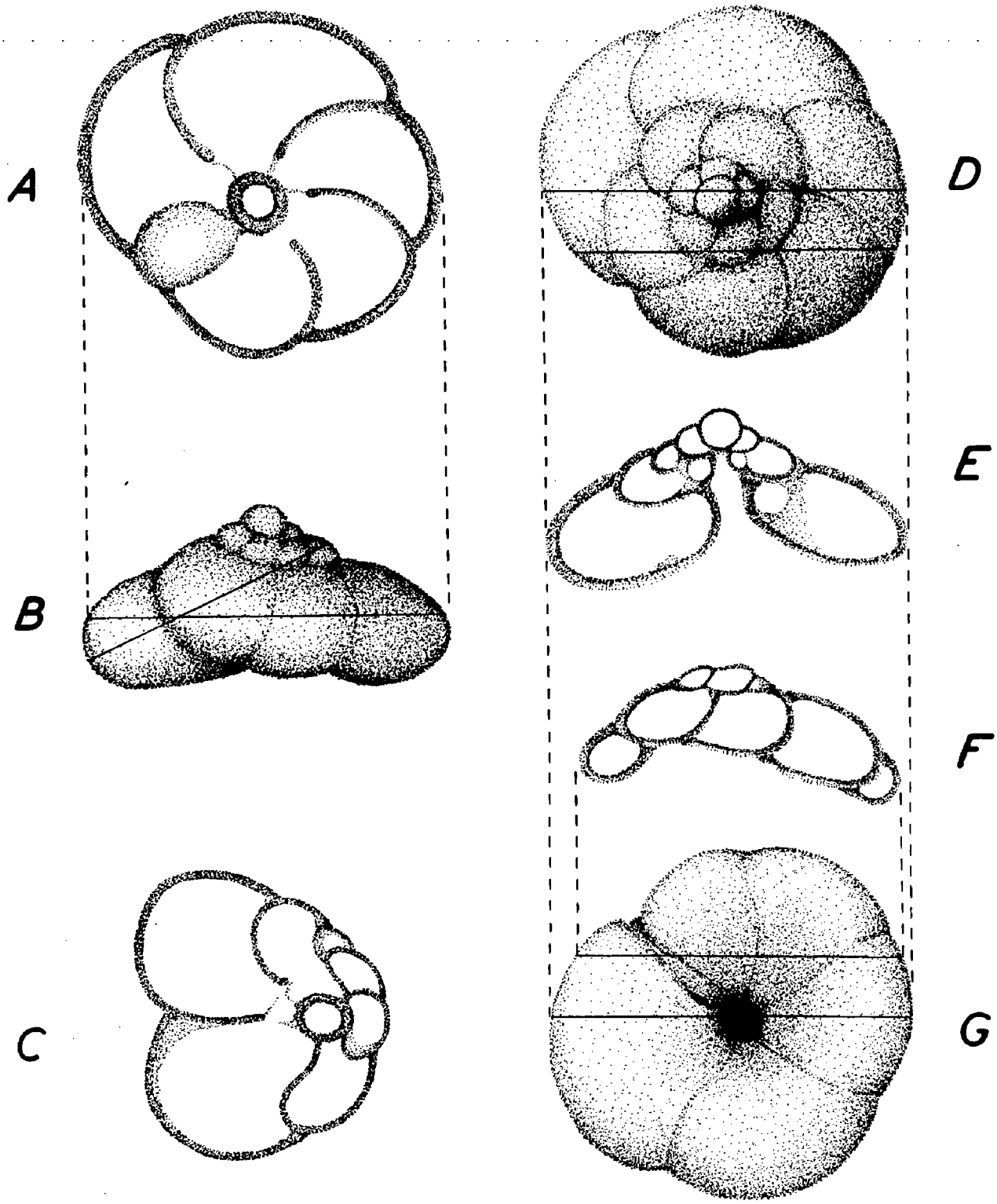
D Dorsal view.

E Axial section; note tangential sections of the chambers revealing the aperture adjoin-:ing the umbilicus.

F Parallel axial section.

G Ventral view.

Reconstruction based on study of random sections and camera lucida drawings of specimen ex Slide No.P.35718 in the Brady Collection, British Museum of Natural History, from shales over Top Hosie Lime-:stone, Brankamhall Quarry, East Kilbride, Lanarkshire.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their mode of growth and in their detailed test morphology. As free specimens there is a superficial resemblance in shape and in the texture of the wall of the two forms, but their sutural pattern is quite distinct. (Text figs.10D and 13D). The sagittal sections of Helicospirina and Tetrataxis are diagnostic, for they demonstrate the fundamentally different chamber form, apertural character, and umbilical development in the two genera. (Text fig.10A and 13H). In Helicospirina (Text fig.10A), the most characteristic feature is the circular section through the umbilicus, from which the arcuate septa radiate out, being interrupted adjacent to the umbilicus where the section meets the aperture. The tetrataxid section (Text fig.13H) is distinct in its crescentic chambers with their median projections producing a complex umbilical pattern, which will vary with the number of chambers and their amount of overlap (cf. Text fig.12, Nos.1d, 2d).

In contrast, when observed in axial or parallel axial sections, the two genera reveal a distinct, if partly superficial, similarity of form (Text figs.10E, and 13F). Since the axial (vertical) section is the one commonly used in the diagnosis of tetrataxid species it is probable that the two genera have been confused in the past. More than sixty species and varieties

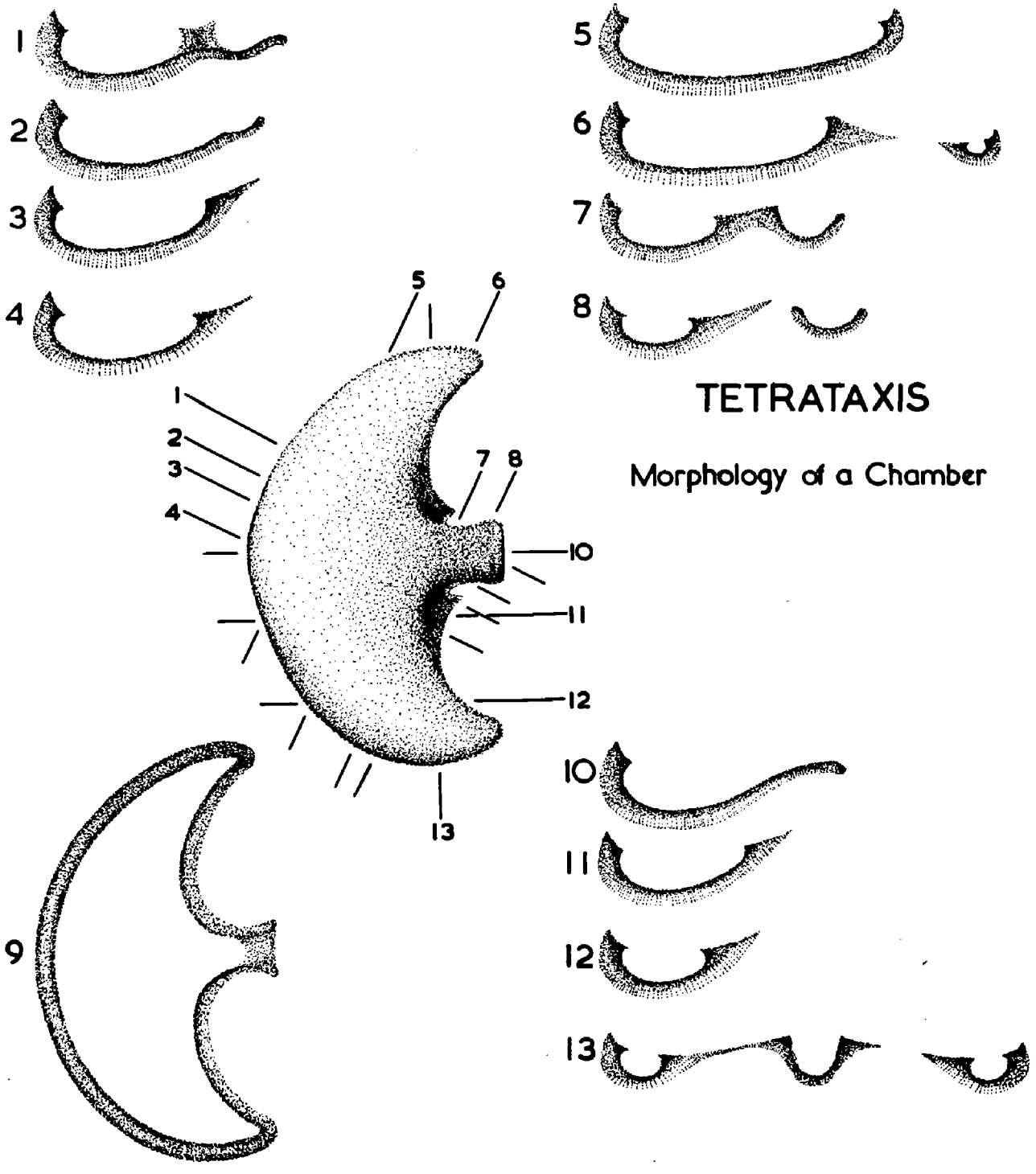
of Tetrataxis have been described on the basis of axial sections only; the criteria for speciation being based mainly on the apical angle, the overall shape of the cone, and the character of the umbilical area. The inadequacies of this taxonomic procedure have been demonstrated by Vasicek & Ruzicka (1957 pp.351-6), who have emphasised the variety of form which can be obtained from axial sections through a single test. The number of chambers in each whorl and their degree of overlap in the umbilical area of the test are regarded by Vasicek & Ruzicka as the most significant morphological characters of Tetrataxis. Moreover, they suggest that the morphology of Tetrataxis can only be adequately reviewed from free specimens. This, however, is an extreme view, for, although it is recognised that a single axial or sub-axial section is inadequate, the value of saggital (horizontal, transverse) sections has generally been disregarded.

It is considered that by reviewing sagittal sections in association with axial sections, it is possible to deduce correctly the three dimensional character of these genera. Such a reconstruction is illustrated for Helicospirina in Text fig.10.

In Tetrataxis, while a sagittal section reveals the number of chambers at only a single point in the spire, nevertheless, it discloses the shape of the

TEXT - FIG.11.

Morphology of a single chamber of Tetrataxis showing its appearance when cut in a variety of planes of section. Sections 1, 2,7,8 and 10 show the varying appearance of sections in the axial zone of the chamber. Section 9 is a sagittal or horizontal section of the chamber, and the remaining sections, 3-6, and 11-13, lie outside the axial zone of the chamber, and their appearance in random sections indicates that the test has been cut parallel or oblique to its axis.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TETRATAXIS
Morphology of a Chamber

TEXT - FIG.12.

Tetrataxis

Comparison of the morphology of forms with three or four chambers in the spire and showing the varying appearance of the axial sections depending on their attitude to the spire. The sections can be defined in terms of the types of sections illustrated in text-figure 2, and so the nature of the spire analysed.

1a. Axial section showing sections of type 8:10.

1b Axial section showing sections of type 1-2:2.

1c Parallel axial section with chamber sections of type 13:11-12.

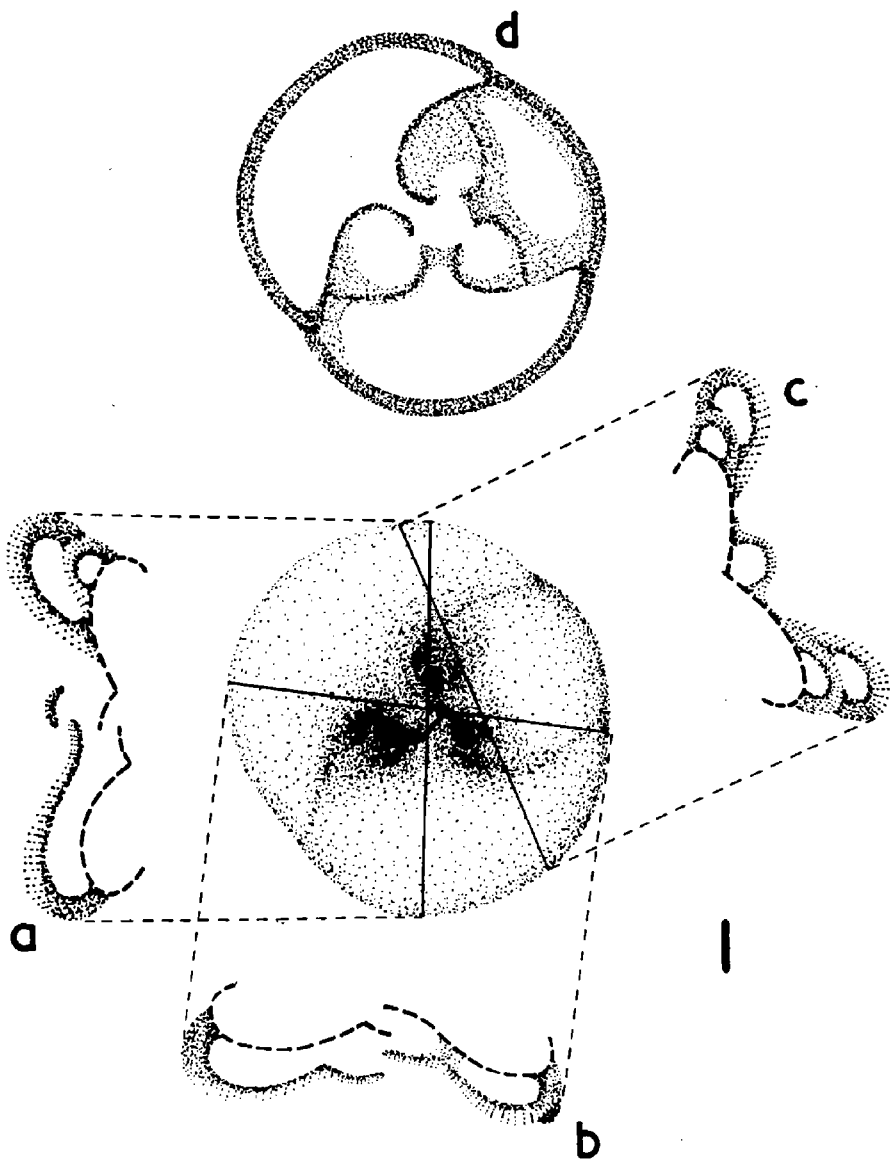
1d Sagittal section revealing complex lobate umbilicus.

2a Axial section showing chamber sections of type 10:10.

2b Parallel axial section, with sections 13 and 12:12.

2c Axial section showing chamber sections of type 1:1 and 8:8.

2d Sagittal section.



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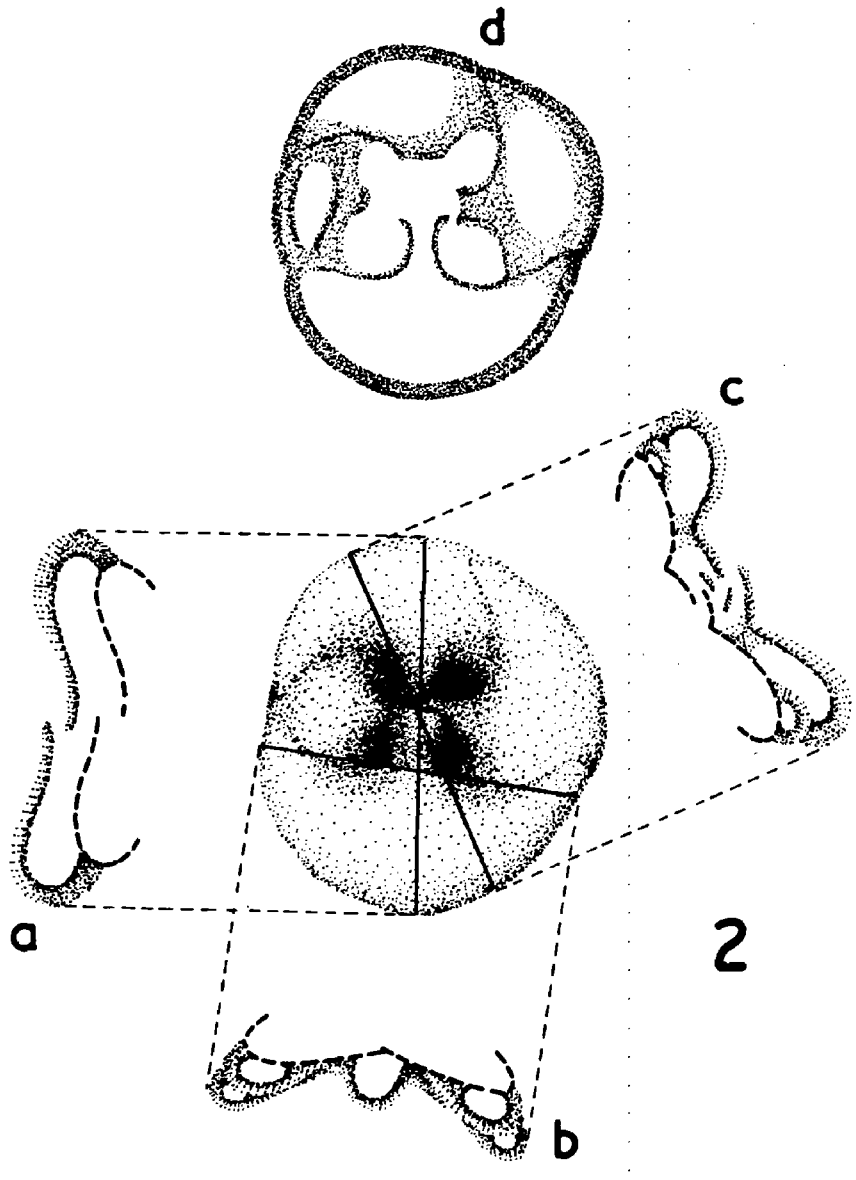

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chambers, their degree of overlap, and their position in relation to the umbilicus (Text fig.12, Nos.1d & 2d). Having regard to this information, and with a detailed analysis of the morphology of a single chamber as it appears in random sections, (Text fig.11), it is possible to elucidate the main characteristics of the spire.

For example, it follows from the morphology of a chamber in Text fig.2, that a section of type 10, opposed to one of type 8, indicates a chamber arrangement in which the median axes of the chambers are at an angle of 120 degrees. Two sections of type 10 would suggest chambers with their axes diametrically opposed. Both situations are illustrated in Text fig.12, Nos.1a & 2a, along with the reconstructed chamber arrangement. It should be noted, however, that the reconstruction cannot satisfactorily be made unless the shape and probable overlap of the chambers is known from sagittal sections (Text fig.12, Nos.1d,2d). Furthermore, it can be seen that where three chambers are arranged in each whorl, the sections will always differ on opposite sides of the spire (Text fig.12 Nos.1a & 1b), while in a spire with four chambers regularly arranged similar sections will be obtained on each side of the spire (Text fig.12, Nos.2a & 2c). The success of such an analysis is entirely dependant

chambers, their degree of overlap, and their position in relation to the umbilicus (Text fig.12, Nos.1d & 2d). Having regard to this information, and with a detailed analysis of the morphology of a single chamber as it appears in random sections, (Text fig.11), it is possible to elucidate the main characteristics of the spire.

For example, it follows from the morphology of a chamber in Text fig.11, that a section of type 10, opposed to one of type 8, indicates a chamber arrange-:ment in which the median axes of the chambers are at an angle of 120 degrees. Two sections of type 10 would suggest chambers with their axes diametrically opposed. Both situations are illustrated in Text fig.12, Nos.1a & 2a, along with the reconstructed chamber arrangement. It should be noted, however, that the reconstruction cannot satisfactorily be made unless the shape and probable overlap of the chambers is known from sagittal sections (Text fig.12, Nos.1d,2d). Furthermore, it can be seen that where three chambers are arranged in each whorl, the sections will always differ on opposite sides of the spire (Text fig.12 Nos.1a & 1b), while in a spire with four chambers regularly arranged similar sections will be obtained on each side of the spire (Text fig.12, Nos.2a & 2c). The success of such an analysis is entirely dependant

on an accurately median axial section, for the spires of the examples shown in Text fig.12 cannot be differentiated in parallel axial sections Nos.1c and 2b.

A complicating factor in such analyses is the fact that the axes of the tetrataxid chambers are not entirely symmetrically arranged, as is demonstrated in the chamber arrangements shown in Text figs.13 and 14. Nevertheless, by studying sagittal sections along with an analysis of a well centred axial section, it should be possible to deduce the number of chambers in each whorl throughout the spire. Thus, for example, in Text fig.14, there are three chambers in each whorl, but the axis of the chambers in successive whorls follows a shallow helical coil, (note chambers 3, 6, 9, 12, 15 & 18 in Text fig.13B). An axial section in such a specimen should show a constantly changing aspect in chambers throughout the spire. In contrast, Text fig. 13F and G, shows a repetitive character in chambers throughout the spire, while the divergence of the chamber axes from diametrically opposite positions is slight, allowing the inference that there are four chambers in each whorl, with the axis of the chambers insignificantly displaced in each successive whorl.

Although the bulk of species of Tetrataxis described from random fragments in thin section are not

TEXT - FIG.13.

Tetrataxis.

A Ventral view showing typical preservation with umbilicus and aperture obscured by matrix.

B Lateral view showing the arrangement of the chambers, four in each whorl.

C Lateral view.

D Dorsal view.

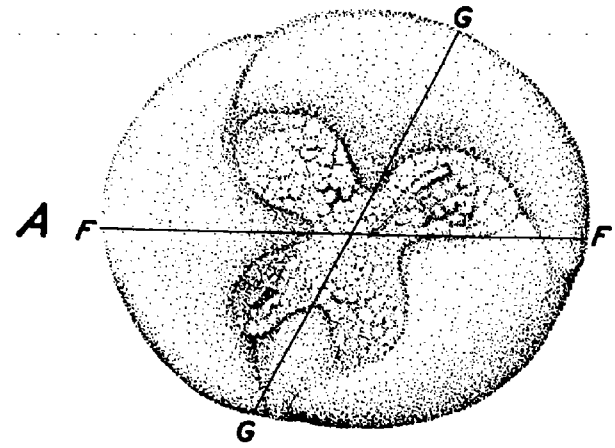
E Ventral view showing the character of the umbilicus with overlapping valvular projections. Note the complexity of the aperture, arising as a pore at the base of each umbilical depression and continuing slit-like beneath the sub-tubular valvular projections.

F Axial section in plane shown in D.

G Axial section in plane shown in D.

H Sagittal section through final whorl.

Reconstruction based on the study of random sections and camera lucida drawings of specimens on slides F.431/1 and P.431/2 in Hunterian Museum of the University of Glasgow, from Coral Limestone, Corrieburn, near Kirkintilloch.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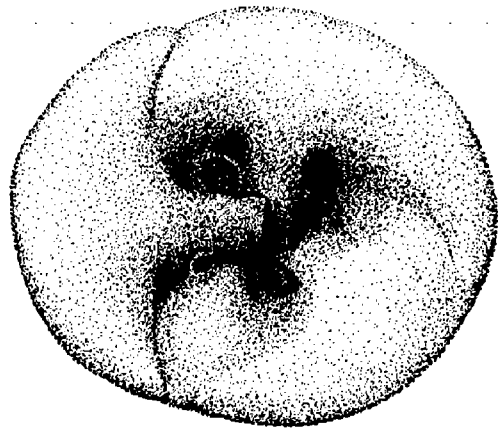
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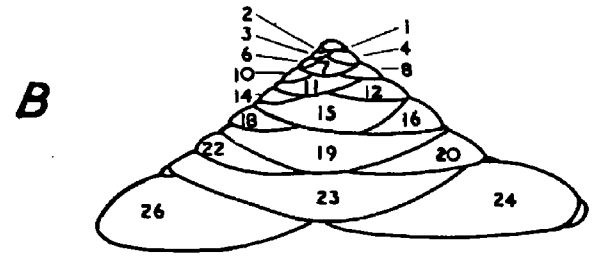
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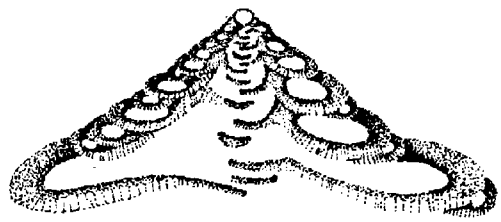
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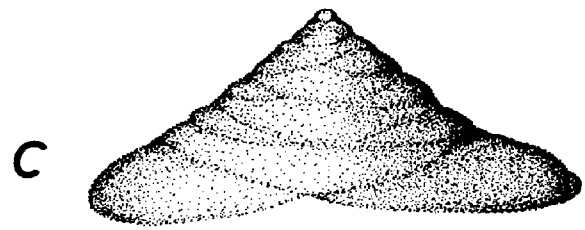
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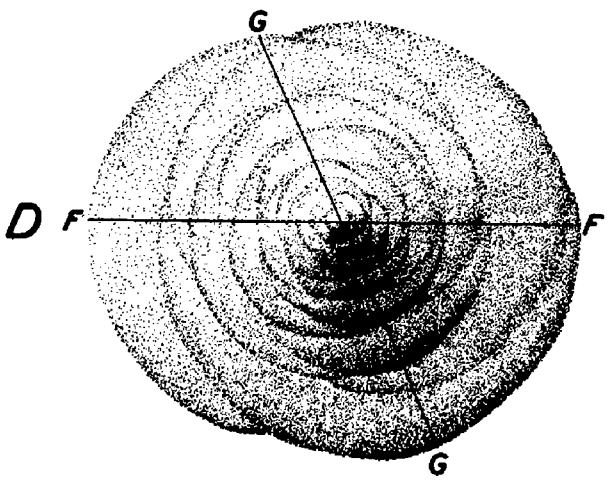
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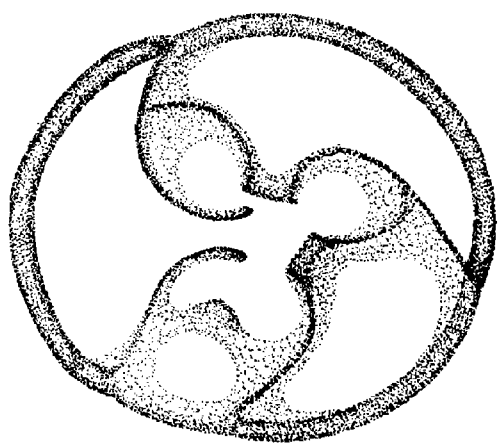
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axial and do not pass through the apex of the test, current descriptions give considerable weight to the apical angle which may, indeed, have some taxonomic value when measured on axial sections. However, even then, in many cases, it is subject to considerable variation depending on the attitude of the specimen to the bedding planes during consolidation and compaction of the host sediment.

The present systematic treatment leads to species determined from random sections, whose characters are basically governed by the manner in which the section is cut from the solid specimen. Thus Tetrataxis hemisphaerica Morozova, 1949, is based on an oblique section which does not cross the axis of the test, while Tetraxis hemisphaerica var. elongata Morozova 1949, is a section crossing the axis of the test, and similarly T. angusta Vissarionova, 1948, is based on sections cutting the lateral slopes of the test at a low angle. Oblique sections should be readily recognised by their failure to reveal details of aperture, or valvular projections, and, furthermore, the chambers will characteristically be cut in sections of the type 3, 6, 12 and 13, in Text fig.11.

The number of chambers appearing in an axial section of Tetrataxis depends on the manner in which the section bisects the spire as will be seen from examination of

Text fig.4F and G, which show a range from 7 to 10 chambers on one side of the spire in a form which has 6 whorls. A similar comparison can be seen in Text fig.14A and C. It is, therefore, entirely misleading to count the chambers visible in order to determine the number of whorls as has been done by Rauser-Chernoussova, 1948, Vissarionova 1948, and others. This procedure is entirely inadequate, and a proper determination of the number of whorls cannot be obtained without an analysis of the spire, as has been outlined above.

The result of the present study suggests that the great majority of the described species of Tetrataxis require revision before their true taxonomic position can be determined.

Records of Trochammina from the Palaeozoic are relatively scarce, and from the Carboniferous only four species have been described to date, T. arenosa Cushman & Waters 1927, T. grahamensis Cushman & Waters 1930, T. hasdoensis Bhatia & Singh 1959 and T. ohioensis Conkin 1961.

All these species have been described from free specimens and so far Trochammina has not been recognised in random sections. Currently material has been found that shows that fundamentally Trochammina is structur-:ally similar to the new genus Helocospirina, and its random sections (Plate 26, figs.1-16) are closely

similar to those in Text fig.10A, C, E and F. Thus sections figured by Termier & Termier (1950, Plate 1, figs.23-25) as Globivalvulina bulloides (Brady) are possibly referable to Trochammina or Helicospirina depending on their wall structure.

Current research on Palaeozoic agglutinate foraminifers suggests that they have a siliceous cement. Most of the authors working in this field have been reluctant to accept that this could result from secondary silicification, despite the fact that a considerable amount of material has been obtained from acid residues. Indeed, Conkin (1961 p.316), has argued that the only valid basis for generic differentiation of isomorphous foraminifers is the nature of the cement, while he considers the nature, presence or absence, of agglutinate grains merely a specific character. Thus, in the present case Trochammina scotica sp. nov. with an agglutinate wall, the particles bound by a ferrugenous-calcareous cement, could be regarded as a genus distinct from T. ohioensis Conkin (1961), reputedly with a siliceous cement. By the same argument T. scotica must be regarded as a synonym of Helicospirina, both having a calcareous wall.

These views, however, are not accepted for, as Cummings (1955) has pointed out, variety of wall

structure is a direct product of differing metabolic function and mode, and hence a reliable basis of morphological classification. Thus there are few authors who would now consider the synonymy of the structural isomorphs Endothyranella (secreted test) and Ammobaculites (agglutinate test) as Conkin (1961 p.319) and Ireland (1956 p.389) has discussed. It is, therefore, contended that a wholly secretional test may be validly differentiated from an agglutinate isomorph, though both have a calcareous basis. Such a conclusion is, of course, strengthened in the case of Helicospirina by its compound wall structure, which emphasises its fundamentally secretional nature as opposed to the simpler agglutinate wall structure of Trochammina.

The nature of the cement may ultimately provide a basis for generic differentiation but the role of secondary replacement is not yet fully understood, and few studies have included satisfactory petrographic study of the wall structure and its enclosing host sediment. Thus, Terriere (1963), in studying the petrography of Upper Pennsylvanian limestones of Central Texas, has reported the widespread occurrence of authigenic quartz, and quite extensive replacement of the wall of calcareous foraminifers by silica; apparently occurring at a very early phase in the

diagenetic history of the limestone. These are features which were entirely overlooked by Cushman & Waters (1930) in their study of the foraminifers from the same area. Similarly, Ireland (1956 p.838) considered that secondary silicification played an insignificant role, and maintained that silicified calcareous forms could be differentiated from originally siliceous ones.

It has been shown by Hedley (1963) that the cement of recent foraminifers has an organic basis which may be mineralised by carbonate, iron, or possibly by silica. It is not yet fully established whether the mineral matter is of entirely secretory origin, and it is possible that silica may represent very early replacements of the test on the sea bottom, or even during life. Consequently the chemical composition of the cement in agglutinate foraminifers is not a character of prime systematic significance.

SYSTEMATIC DESCRIPTIONS.

In most previous classifications the Tetrataxidae, and the Biseriamminidae, where recognised, have been placed within the super-family Lituolacea, or linked closely with the Trochamminidae; a classification which stems initially from Cushman's (1927, 1948 p.206) view that Tetrataxis, Globivalvulina, and numerous other Carboniferous genera had an arenaceous wall. The erroneous nature of this concept was discussed by Galloway (1933), whose placing of the Tetrataxinae within the Endothyridae is more in keeping with the classification followed below. Subsequent authors have apparently been influenced mainly by the chamber arrangement and form of the test, (Glaessner, 1945 p.106 and Sigal, 1952) although Rauser-Chernoussova & Fursenko (1959 p.221) recognised the artificial, and largely conventional nature of their grouping of the families Tetrataxidae and Biseriamminidae in the order Ataxophragmida. It has been argued by Pokorny (1958 p.165) that the contrasts in wall structure, which have systematic value in modern families of foraminifers, have developed and become accentuated during phylogeny, and that in more primitive groups of foraminifers, particularly those with unilocular tests, the wall is subject to gross variation in

structure depending upon environment. Consequently, Pokorny believes that chamber arrangement and form of the test is of greatest significance in interpreting phylogeny and classification of primitive families of foraminifers where gradations from agglutinate to wholly secreted walls are recorded.

In the case of Tetrataxis there is no evidence to suggest that it could have developed from an agglutinate isomorph, and the wall structure of this genus is highly distinctive in character and possibly unique in structure. Analogous granular calcareous walls are known in the super-family Endothyracea, but with the possible exceptions of the Lasiodiscidae and the Archaediscidae, they differ strikingly in fine texture. Thus, it is considered that the Tetrataxidae and the Biseriamminidae should be excluded from the Endothyracea although they may still find a place within the sub-order Fusulinina.

The new genus Helicospirina has a wall typically tetrataxid in structure and texture and it is, therefore, confidently assigned to the Tetrataxidae, although, in shape, it resembles Trochammina more closely. The phylogenetic relationships of Helicospirina and Tetrataxis are as yet uncertain but, in so far as Helicospirina has the simpler test architecture, it may prove to be closest to the ancestral form.

F O R A M I N I F E R A

Sub-Order FUSULININA Wedekind, 1937.

Family TETRATAXIDAE Galloway, 1933.

HELICOSPIRINA gen. nov.

Type Species:

Valvulina plicata Brady 1876, p.88,
Plate IV, figs.10a,b.

Description:

Test free or attached, trochospirally coiled with a low spire, umbilicate, all chambers visible on the convex dorsal side, only those of the last whorl visible on the concave ventral side; chambers, 4-7 in a whorl, approximately triangular, expanding from umbilicus to periphery, usually overlapping beyond periphery of previous whorl; umbilicus narrow, tubular, extending throughout test; sutures strongly curved dorsally, running smoothly into the curve of the periphery, ventrally, sutures slightly curved meeting periphery radially; wall granular calcareous, sometimes with fibrous layer developed on the ventral part of later whorls; aperture ventral, circular to semi-circular, at the base of the last chamber adjacent to the umbilicus; proloculum spherical.

In thin section the diagnostic features of this genus are, its wall structure which is tetrataxid in character, but lacks the well developed 'fibrous' layer; and the narrow circular umbilicus which is most distinctly seen in sagittal sections, but can be

observed in perfect axial, or some oblique sections.

Ontogeny:

So far no evidence of dimorphism has been observed, and the genus appears to develop from a simple spherical proloculum and reach the adult condition without any significant morphological change.

Comparison and Affinities:

This genus may be differentiated from Trochammina, with which it is an isomorph, by the different wall structure. It is most closely related to Tetrataxis but differs notably in chamber form, apertural character, and in the narrow central umbilicus. In detail, sagittal sections can be differentiated from those of Tetrataxis by their radiate septa, and the central circular cross section of the umbilicus, (Text fig.10A), while axial sections reveal tha narrow umbilicus with the adjoining circular apertures. (Text fig,10E).

Parallel axial and oblique sections of Helicospirina (Text fig.10C and F) have been identified as Globivalvulina, (Cummings 1961, Termier & Termier 1950) but such sections can be differentiated from the latter genus by their lack of biseriality, and comparison with a typical globivalulinid morphology such as that so excellently figured by Reichel 1945,

immediately emphasises their simple trochoid character.

A sagittal section of Helicospirina was figured by Davis (1951, Plate II, fig.7) as an approximately equatorial section about the third whorl of Howchinia showing septa. Such an interpretation is clearly incorrect since there is no evidence to suggest that Howchinia is septate at any stage in its ontogeny.

Preservation and Matrix:

As Brady (1876) recognised in his discussion of Valvulina plicata many of the specimens tend to be poorly preserved. Crushing and distortion of tests during fossilisation leads to collapse of the spire while the chambers of the last whorl are flattened and spread out laterally producing an abnormally discoid test. The thinner wall of this genus possibly renders it more prone to distortion than the more stoutly buttressed wall of Tetrataxis.

Horizon and Facies:

A single record of Helicospirina exists from the Lower Pennsylvanian of the United States (Warthin, 1930) and its occurrence has been confirmed only from the upper part of the British Visean and Lower Namurian. It is considered that revision of the following records may extend the range and distribution of this genus:-

Globivalvulina bulloides (Brady) in Termier & Termier 1950, Plate 1, figs.23-25.

Globivalvulina sp. in Cummings, 1961.

Tetrataxis minima Lee & Chen, in Termier & Termier, 1950, Plate 1, fig.29.

Tetrataxis eominima Rauser-Chernoussova, 1948. Plate 3, fig.11.

Rauser-Chernoussova, in Malakhova, Plate V, fig.6.

Tetrataxis expansus Malakhova, 1956, Plate XIV, figs.2, 3.

Tetrataxis sussaicus Malakhova, 1956, Plate V, fig.6.

Tetrataxis digna Grozdilova & Lebedeva, 1954, Plate VIII, fig.3.

Tetrataxis plicata Warthin, 1930, p.25, Plate 1, fig.18.

HELICOSPIRINA PLICATA (Brady)

Plate 22, Figs.1-7.

Valvulina plicata Brady, 1873 (nom. nud.).

" " Brady, 1876, p.88, Plate IV, figs.10a,b.

Description:

Test free, trochoid, spire low, apical angle from 120 to 130 degrees, up to four whorls, all chambers visible on dorsal side; umbilicus narrow, tubular, extending throughout test; chambers typically five in a whorl, usually overlapping onto or beyond the periphery of previous whorl, in sagittal sections, triangular, broadly rounded at the periphery, in axial sections expanding from umbilicus to periphery with a flat to slightly convex ventral surface meeting broadly rounded dorsal surface acutely; periphery of last whorl almost circular, slightly lobulate, sutures very slightly depressed, on dorsal surface curved, sweeping into periphery, ventrally almost straight radial; wall thin, granular, often with thin 'fibrous' layer on ventral surfaces of later whorls; aperture, ventral, interiomarginal, a circular to semi-circular opening adjacent to the umbilicus.

Dimensions:

	Diameter (mm.)	Height of Spire (mm.)
Holotype	0.47	0.14
Paratype 1 (last whorl)	0.44	0.19
3rd whorl	0.28	0.12
2nd whorl	0.20	0.08
1st whorl	0.09	0.03
Paratype 2	0.30	-

Depository:

British Museum (Natural History), Holotype on slide No.P.35444 (Brady, 1876, Plate IV, fig.10a, b), from shales above the Main Limestone, Lower Limestone Group, Lower Carboniferous, of Brockley, near Lesmahagow, Lanarkshire, Scotland, and Paratypes on slides P.45501 and P.45500, from shales over Top Hosie Limestone, Lower Limestone Group, Lower Carboniferous, of Brankumhall Quarries, East Kilbride, Lanarkshire, Scotland.

Comparison and Affinities:

Externally this species is similar to species of Trochammina known, though rarely, from the Carboniferous. It can be separated from these forms by means of its wall structure, and, in addition, it differs from Trochammina scotica sp. nov. in its lower spire, with fewer chambers in each whorl.

Preservation and Matrix:

The main characteristics of this species have been covered in the generic discussion above.

Horizon and Facies:

The records of Brady (1876) show that this species ranges through the upper part of the British Visean, while the present study confirms it occurrence in the Upper Limestone Group, Namurian of Scotland.

TETRATAXIS Ehrenberg, 1854.

Valvulina (pars) Brady 1876, (non d'Orbigny, 1826).

Ruditaxis Schubert, 1921.

Pseudotetrataxis Marie, in Deleau & Marie, 1961.

Falsotetrataxis Marie, in Deleau & Marie, 1961.

Type Species:

Tetrataxis conica Ehrenberg, 1854 p.24.

Description:

Test free or attached, trochoid, usually with numerous whorls, forming high to shallow discoid cone, dorsal surface convex, ventral surface concave umbilicate; umbilicus subdivided, lobate, with overlapping chambers or open with marginal chambers; chambers crescentic, in the early stages usually three or four to a whorl, often increasing or decreasing in number in later whorls, with a median sub-tubular, to conical projection culminating in a valvular plate or flap extending towards or over the umbilicus; sutures typically shallow, indistinct; aperture complex, umbilical, intercameral at base of each umbilical depression, and continuing slit-like beneath valvular plates, modification varying with degree of overlap of valvular plates; wall calcareous, typically thick, two layered, a rather coarse granular, darker, upper layer, and clear 'fibrous' layer

forming thick buttresses on ventral surface; buttresses often thin or absent in early stages becoming more massive in adult stages.

In thin section this genus can be recognised by its rather characteristic wall structure together with its conical form. In both axial and sagittal sections the chambers opening into the umbilicus through valvular projections are characteristic.

Ontogeny:

It has been suggested that Tetrataxis in its initial stages consists of a proloculum and an elongate second chamber (Cushman 1927, Cushman & Waters 1930, p.74. Cushman 1950, p.206 and Pokorny 1963, p.211). This would seem to be a misinterpretation initiated by Moeller's (1879) confusion of the genera Tetrataxis and Howchinia (T. gibba Moeller), together with the difficulty normally experienced in observing the earliest stages of Tetrataxis. While it is possible that such a structure may be present in some species of this genus, much of the evidence, including the present study, suggests that the test is chambered throughout.

As the name suggests, Tetrataxis in its typical form has four chambers in each whorl. Moeller (1879) and Brady (1876), have noted that some forms showed three or sometimes five chambers in a whorl, but they

did not regard this variation as significant. More recent studies (Vasicek & Ruzicka, 1957), together with present results, suggest that such changes in ontogeny may be of systematic importance.

Possibly of greater significance than the numerical arrangement of the chambers is their position in relation to the umbilicus. In one group of forms, T. scutella Cushman & Waters, T. corona Cushman & Waters, T. concava Galloway & Ryniker, and similar species, chambers become withdrawn from the axis of the test leaving an open umbilical cavity while, in others, T. quadriloba sp. nov., T. nemejci Vasicek & Ruzicka and T. tricamerata sp. nov., the umbilicus remains closed by overlapping valvular plates producing a complex labyrinthic umbilical zone in the test. It is possible that further research may show this distinc-:tion to have generic significance.

Comparison and Affinities:

The chamber form of Tetrataxis (Text fig.11) is probably its most distinctive character, and it should normally be sufficient to distinguish it from other genera.

Polytaxis was considered to be distinct from Tetrataxis by Cushman & Waters (1928), on the basis of its multichambered form with the chambers withdrawn

from the axis of the test to produce a very broad shallow umbilical depression. This structure appears to be the final stage of a bioseries in which the chambers withdrew from the umbilicus and gradually increase in number. It is possible that generic rank should be applied to this phyletic line as has been discussed above.

Tetrataxis differs from Helicospirina in the crescentic form of its chambers and in the manner in which the chambers open into the umbilicus beneath a subtubular valvular projection or flap.

Preservation and Matrix:

One of the typical features of preservation of Tetrataxis is the infilling of the umbilical cavity with matrix (Text fig.12A), so that it is rare to observe the true character of the umbilicus and aperture. Furthermore, it is commonly extremely difficult to detect the sutures on the ventral surface of the test. These conditions, in general, have led to misinterpretations of the chamber form and apertural character of this genus, such as the reconstruction of Reitlinger, 1950. Fortunately, it has been possible to obtain some specimens relatively free of matrix, and, from the study of sections, it is clear that the aperture has the form illustrated in Text fig.12E.

Crushing and distortion during fossilisation lead to the accentuation and depression of the conical shape of the test, depending on the attitude of the test to the bedding planes during compaction. Lateral pressure on the test leads to flattening and infolding of the lateral walls of the chambers, narrowing the apical angle and heightening the spire. Vertical compression leads to deflation of chambers in later whorls, and the apex becomes forced downwards into the lower chambers, causing them to spread laterally, leading to an increase in the apical angle and a decrease in the height. Failure to appreciate distortion of this character led Brady (1876) to describe the variety T. palaeotrochus var. compressa (compressed laterally) and T. decurrens (compressed vertically). In some cases the apparent scale-like nature of the tetrataxid test is accentuated through the loss of its apex; a feature, which is particularly common in material extracted from shales, and apparently resulting from their maceration and disintegration.

Some of Brady's (1876) records of T. decurrens are based on broken specimens of this type, while Valvulina rudis Brady, type species of Ruditaxis Schubert, 1921, appears to be based on a partly crushed and broken tetrataxid together with crushed specimens whose affinities are not clear.

Horizon and Facies:

Tetrataxis occurs throughout the greater part of the Carboniferous and Permian, and recently it has been recorded from the Rhaetic of Europe (Kristan, 1957). It occurs particularly abundantly in argillaceous bioclastic facies, although Cummings (1961) has also reported a tendence for tetrataxids to occur abundantly in sandy limestones.

TETRATAXIS QUADRILOBA sp. nov.

Plate 22, Figs.8-12.

Valvulina palaeotrochus Brady, 1876, p.83, Plate IV, figs.1-4.

Valvulina decurrens Brady, 1876, p. 87, Plate III, figs. 17-18.

Tetrataxis conica (Ehrenberg) - Lizka, 1958, p.166 Plate XVIII, fig.11; Plate XIX, fig.6.

Description:

Test free, (or attached ?), trochoid, conical, apical angle berween 70 and 90 degrees, sides straight to slightly convex, with up to twelve whorls each typically with four chambers, occasionally with five in final whorls of large specimens, ventral surface concave with four lobed umbilicus, divided by over-:lapping valvular projections of chambers; chambers crescentic, each overlapping about one third of previous chamber, not overlapping periphery of previous whorl, ventral surface gently convex with a central tapering sub-tubular lobe curving up into the umbilical cavity, flattening out in zone of overlap with the other umbilical projections; sutures shallow, indistinct; aperture umbilical, complex, intercameral, at base of each umbilical lobe and continuing as a slit beneath the valvular projection opening into the middle of

the umbilicus; wall calcareous, thick, two layered, a rather coarse granular layer forming the main structure of the test, with thick 'fibrous' buttresses on ventral surfaces; buttresses thin or indistinct in early stages, often massive in later stages.

Dimensions:

	Diam. (mm.)	Height (mm.)	Apical ∠	Diam. Prol.	Thickness of Wall, Final Whorl.
Holotype	0.86	0.62	75	-	-
Topotype 1	0.35	-	-	-	0.026
" 2	0.83	-	-	-	0.060
" 3	0.84	0.65	70	-	0.068
" 4	1.05	0.53	85	-	0.060

Depository:

Holotype in British Museum (Natural History) on slide No.P.35441; Topotypes in John Young Collection, Hunterian Museum of the University of Glasgow on slides Nos.P.79/1-4, all from the shales overlying the Main Limestone, Lower Limestone Group, Lower Carboniferous, of Brockley, near Lesmahagow, Lanarkshire, Scotland.

Comparison and Affinities:

When Brady (1876) described this species he regarded it as a synonym of Tetrataxis conica Ehrenberg, 1854, however, he did not use this specific designation

as it was preoccupied by Valvulina conica Parker & Jones. Brady, therefore, chose to use V. palaeotrochus for he considered the material figured by Ehrenberg under the names Textilaria palaeotrochus and Tetrataxis conica to be conspecific. In practice the figures given by Ehrenberg (1854, Plate xxxvii) do not allow more than a generic identification and so their synonymy is dubious. Therefore, the forms which Brady regarded as T. palaeotrochus are here redescribed under the new name T. quadriloba.

Moeller (1879) redescribed Tetrataxis conica from its type locality and it is from this description that its characters are really known. Moeller followed Brady in regarding T. conica and Textilaria palaeotrochus as synonyms, but the present revision shows that Tetrataxis palaeotrochus of Brady differs materially from T. conica of Moeller in internal structure. The axial section figures by Moeller (1879 Plate 7, fig.1) shows that the valvular projections are withdrawn from the axis of the test leaving a narrow free umbilical cavity extending throughout the test. If this section is accurately drawn, as it appears to be since it was refigured in Rauser-Chernoussova & Fursenko (1959, Plate XII, fig.1), then it is in contrast to the overlapping valvular projections and labyrinthic umbilicus of T. quadriloba (cf. Text fig.13 & Plate 22, figs.8-12). It is

believed, therefore, that the differing umbilical form and apertural character provides a means of differentiat-:ing these species.

T. quadriloba closely resembles T. tricamerata sp. nov., T. triloba sp. nov. and T. nemejci Vasicek & Ruzicka, in general shape and in having a closed umbilical cavity with overlapping valvular projections, but it can be differentiated from these species through the arrangement of its chambers, four in each whorl through-:out growth. In some cases the overlap of the chambers is such that the ventral surface is circumscribed by three chambers (Text fig.13A & E), but this species may still be recognised by the four diametrically opposed valvular projections.

Preservation & Matrix:

Lower Carboniferous records of T. palaeotrochus var. compressa and T. decurrens (Brady) appear to be based on crushed, deflated, and broken specimens of this species.

Horizon and Facies:

An abundant form in bioclastic shale and limestone facies in the middle and upper part of the British Visean. It occurs as a rare form in the Index Limestone, at the base of the Upper Limestone Group, Namurian of Scotland.

TETRATAXIS TRICAMERATA sp. nov.

Plate 23, Figs.1-6; Plate 24, Figs,1-4.

Description:

Test free, (or attached ?), trochoid, conical, apical angle between 70 and 90 degrees, sides straight to slightly convex, with up to 10 whorls, each typically with three chambers, ventral side concave with trilobed umbilicus; chambers crescentic, each typically overlapping half of previous chamber, broadly rounded peripherally, not overlapping beyond periphery of previous whorl, ventral surface convex, with a central tapering sub-tubular lobe curving up into the umbilical cavity, flattening out in the zone of overlap with the other valvular projections; sutures shallow, indistinct; aperture complex, opening into umbilicus, intercameral at the base of each umbilical lobe, continuing as a slit beneath the valvular projection, opening into the middle of the umbilicus; wall calcareous, thick, two layered, rather coarse granular layer forming the main structure of the test with thick 'fibrous' buttresses on ventral surfaces; buttresses thin or indistinct in early stages, often massive in adult stages.

Dimensions:

	Diam. (mm.)	Height (mm.)	Apical ∠	Thickness of Wall Final Whorls.
Holotype	0.73	0.50	80	-
Paratype 1	0.43	-	-	-
Paratype 2	0.93	0.60	80	0.043

Depository:

Hunterian Museum of the University of Glasgow, Holotype slide No.P.425, from shales over Orchard Limestone, Poniel Water, Coalburn, Lanarkshire. Paratype 1 on slide No.P.426/1 from shales over Lyoncross Limestone, Whitecraigs, Renfrewshire, and Paratype 2 on slide No.P.427/1 from shale parting in the Orchard Limestone, Craigburn, Lanarkshire. All from the Upper Limestone Group, Namurian of Scotland.

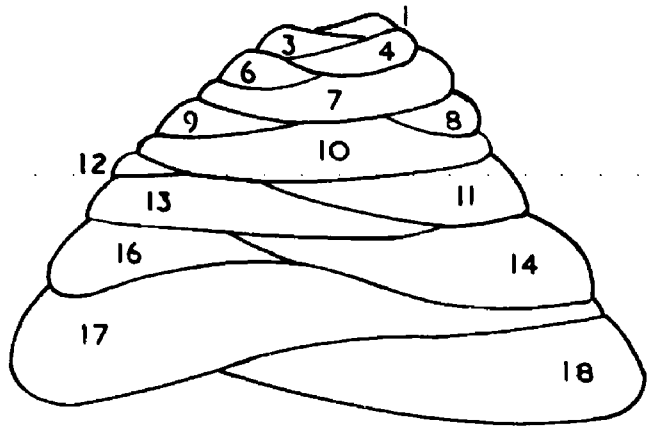
Comparison and Affinities:

This species is identical to T. quadriloba in all its principal morphological features, but it can be differentiated from the latter species in having three chambers in each whorl, with the axes of successive whorls describing a shallow helical spire (Text fig.14), a feature which distinguishes this species also form T. nemejci Vasicek & Ruzicka. T. tricamerata differs from T. triloba sp. nov. mainly in having distinct 'fibrous' buttresses.

TEXT - FIG.14.

Tetrataxis tricamerata sp. nov.

Diagram of chamber arrangement based on camera lucida drawings of the holotype. (see Plate 24, figs.1-4).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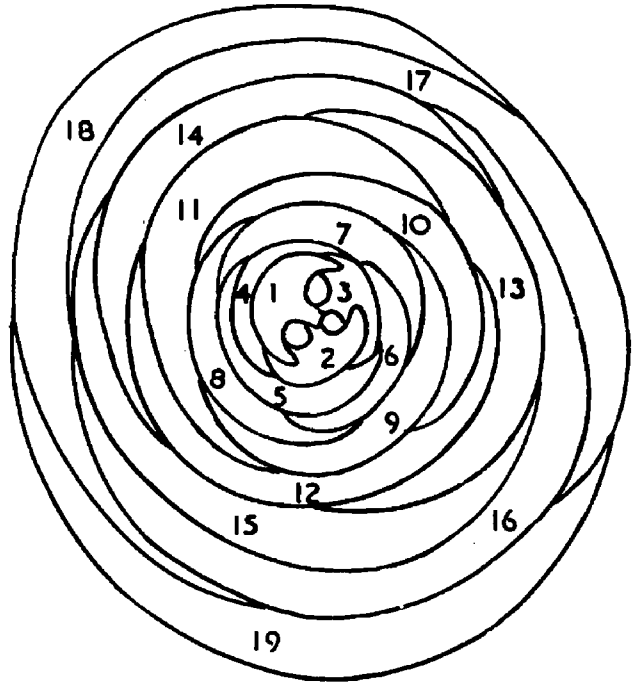
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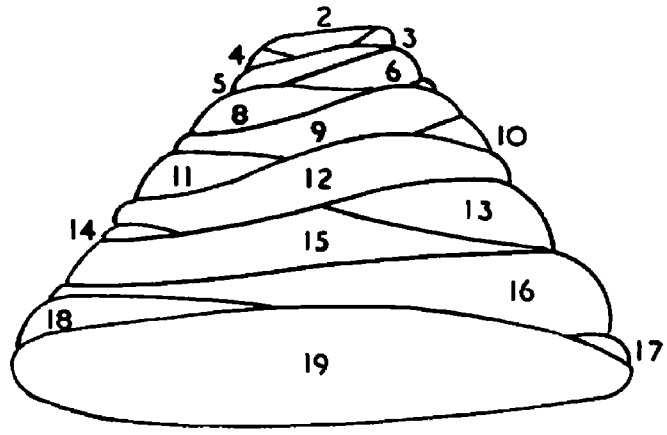
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Preservation and Matrix:

As is typical of tetrataxid tests, this species suffers collapse, distortion and fracturing during fossilisation and records of Valvulina palaeotrochus var. compressa Brady, 1876, and V. decurrens Brady, 1876, in the Upper Limestone Group, Namurian of Scotland are based on broken and crushed specimens of this form.

Horizon and Facies:

A common to very abundant form in bioclastic facies at all horizons within the Upper Limestone Group, Namurian of Scotland, and probably character-:istic of this interval. Records within the Upper Limestone Group of Valvulina palaeotrochus (Ehrenberg) in Brady's monograph (1876) refer to this species.

Measurements of Additional Material:

Prom shale parting Orchard Limestone, Craigburn:-

Specimen No.	Diam.	Height	Apical ∠	Chambers in Last Whorl.
P.427/2	0.32	0.21	90	3
P.427/3	0.37	0.38	70	3
P.427/4	0.48	0.32	80	3
P.427/5	0.39	0.23	90	3
P.427/6	0.74	0.65	75	3
P.427/7	0.90	0.55	80	4

From shale over Orchard Limestone, Strutherhill:-

Specimen No.	Diam.	Height	Apical ∠	Chambers in Last Whorl.
P.428/1	0.56	0.37	70	3
P.428/2	0.46	0.23	85	3
P.428/3	0.38	0.23	90	3
P.428/4	0.48	0.27	105	3
P.428/5	0.34	0.31	70	3

From shale over Lyoncross Limestone, Whitecraigs:-

P.426/2	0.62	0.34	90	3
P.426/3	0.68	0.41	95	3
P.426/4	0.62	0.34	90	3

From Castlecary Limestone, Westerwood.

P.429	0.89	0.68	75	3

TETRATAXIS TRILOBA sp. nov.

Plate 23, Figs.7-14.

Description:

Test free, trochoid, conical, apical angle between 70 and 90 degrees, sides straight to slightly concave, with up to eight whorls, each typically with three chambers, ventral side concave with trilobed umbilicus; chambers crescentic, each overlapping half of previous chamber, rather flat lateral and ventral surfaces with acute peripheral angle, with a central tapering sub-tubular lobe curving up into the umbilical cavity, flattening out in the zone of overlap with the other valvular projections; sutures shallow, indistinct, aperture complex, opening into umbilicus, intercameral at the base of each umbilical lobe, continuing as a slit beneath valvular projections, opening into the centre of the umbilicus; wall calcareous, thin, single layered, consisting of a dark, rather coarse, granular layer without distinct 'fibrous' buttresses.

Dimensions:

	Diam. (mm.)	Height (mm.)	Apical ∠	Diam. Prol.	Thickness of Wall, Final Whorl.
Holotype	0.71	0.37	90	-	0.017
Paratype 1	0.60	0.32	90	-	0.026
" 2	0.48	0.34	90	-	0.017

	Diam. (mm.)	Height (mm.)	Apical ∠	Diam. Prol.	Thickness of Wall, Final Whorl.
Paratype 3					
Whorl 1	0.085	0.048	80	0.026	0.006
Whorl 2	0.136	0.077	80	-	0.009
Paratype 4	0.65	0.38	90	-	0.023
Paratype 5	0.34	-	-	-	0.017
Paratype 6	0.47	-	-	-	0.020

Depository:

Hunterian Museum of the University of Glasgow, Holotype slide No.P.430/1, and Paratypes 1-6 on slides Nos.P.430/2-7, all from Castlecary Limestone, Upper Limestone Group, Namurian of Westerwood quarry, neary Castlecary, Dunbartonshire, Scotland.

Comparison and Affinities:

This species is closely similar to T. tricamerata sp. nov., but it can be separated from the latter species by its slender walls without 'fibrous' buttresses; a feature which, in addition to the development of three chambers in each whorl, also distinguishes this species from T. palaeotrochus (Ehrenberg), and T. nemejci Vasicek & Ruzicka.

Preservation & Matrix:

The most striking feature of this species is its

lack of 'fibrous' buttresses, and while the loss of the 'fibrous' layer of a wall has been recorded through recrystallisation (Cummings, 1955), this mechanism has not operated in this case. Specimens of T. tricamerata can be observed closely associated with T. triloba while displaying quite normal thick 'fibrous' buttresses. Furthermore, it is clear that the granular wall in T. triloba is in contact with the ventral surface in each successive whorl in such a way that the 'fibrous' layer could not have been developed. The thickness of the 'fibrous' buttresses in Tetrataxis appears to vary quite considerably, even within a single population, and the variation between populations may have some ecological control as yet not understood. Nevertheless, in the present case, where forms consistently without buttresses occur in association with forms having thick buttresses, it is considered a feature of systematic significance.

Probably because of its more slender wall T. triloba appears more prone to distortion than many other species. The final whorls tend to be compressed and forced out laterally, producing a marked concavity of the lateral slopes which is quite characteristic of this species.

Horizon and Facies:

So far, recorded only from the Castlecary Limestone, Upper Limestone Group, Namurian of Scotland, where it occurs very abundantly in argillaceous bioclastic phases of the limestone in association with rarer specimens of T. tricamerata sp. nov.

Family BISERIAMMINIDAE Chernysheva, 1941.

Genus GLOBIVALVULINA Schubert, 1921.

Type Species:

Valvulina bulloides Brady, 1876, p.89, Plate 4, figs.12-15.

Description:

The characters of this genus have been fully reviewed in the excellent studies of Plummer (1948) and Reichel (1945).

GLOBIVALVULINA BULLOIDES (Brady), 1876.

Plate 24, Figs.6-11. Plate 25, Figs.1-2.

Valvulina bulloides Brady, 1876, p.89, Plate 4, figs.12-15.

Globivalvulina ovata Cushman & Waters, 1928, p.65, Plate 8, figs.8a-c and 1930, p.71, Plate 8, figs.6-11.

Globivalvulina minima Reitlinger, 1950, p.76, Plate 16, fig.14.

Globivalvulina kamensis Reitlinger, 1950, p.78 Plate 16, figs.5,6.

Description:

Test free, small, hemispherical, consisting of biserially arranged chambers in a rapidly expanding,

shallow helical spire of about one and a half whorls, usually with five to six pairs of chambers, occasionally with seven pairs; chambers broad, inflated, rapidly expanding in size, slightly compressed dorso-ventrally with flat to concave apertural face; sutures distinct, depressed; wall relatively thick, (17-25 microns in final chambers) dark, with rather coarsely granular texture, sometimes showing clear evidence of radiate structure; aperture low, slit-like, on terminal face of last chamber, with distinct valvular projection extending across opposed aperture and valvular projection of penultimate chamber; septa after initial convexity become flat to concave towards the apertural extremity where septal end is slightly thickened; proloculum, large, spherical thick walled.

Dimensions:

	Diam. Apertural Face (mm.)	Diam. Spire (mm.)	Height Spire (mm.)	Height Last Chamber	Thickness of Wall. (mm.)
Lectotype	0.43	0.43	0.29	0.26	-
Paralectotype 1	0.43	0.41	-	-	0.023
Paralectotype 2	-	0.48	0.30	0.29	0.025
11 chambers	-	0.48	0.30	0.29	0.025
9 chambers	-	0.35	0.20	0.21	0.017
7 chambers	-	0.26	0.14	0.14	0.011
5 chambers	-	0.16	0.10	0.10	0.011

Depository:

The specimen on slide P.41652 in the Brady collection of Carboniferous and Permian Foraminifera, British Museum (Natural Hisotry) is here designated as Lectotype of Globivalvulina bulloides Brady from the Fusulina-beds of the Upper Coal Measures of Iowa, U.S.A. (see Plate 24, figs.5-11 and Text fig.15). This specimen was isolated from syntypes on slide P.35518 by Loeblich & Tappan, but although it is figured (Loeblich & Tappan, 1964 p.C337, fig.255), it was not formally designated as the lectotype. Sections from syntypes ex slide P.35445 in the Brady collection provide Paralectotype 1, P.45679 (Plate 25, fig.1) and Paralectotype 2, P.45678 (Plate 25, fig.2), from the same horizon and locality as the lectotype.

Comparison and Affinities:

Although this species is well known its internal structure has never been fully defined and figured. Its identification in thin sections has been based mainly on the recognition of sections tangential to the dorsal surface such as that figured by Brady (1876, Plate IV, figs.14 and 15.). Reichel suggested that these figures were possibly not of the same species as the figured specimen (Plate IV, fig.12a-c), however, examination of the actual material shows that this suggestion is

TEXT - FIGURE 15.

Globivalvulina bulloides (Brady).

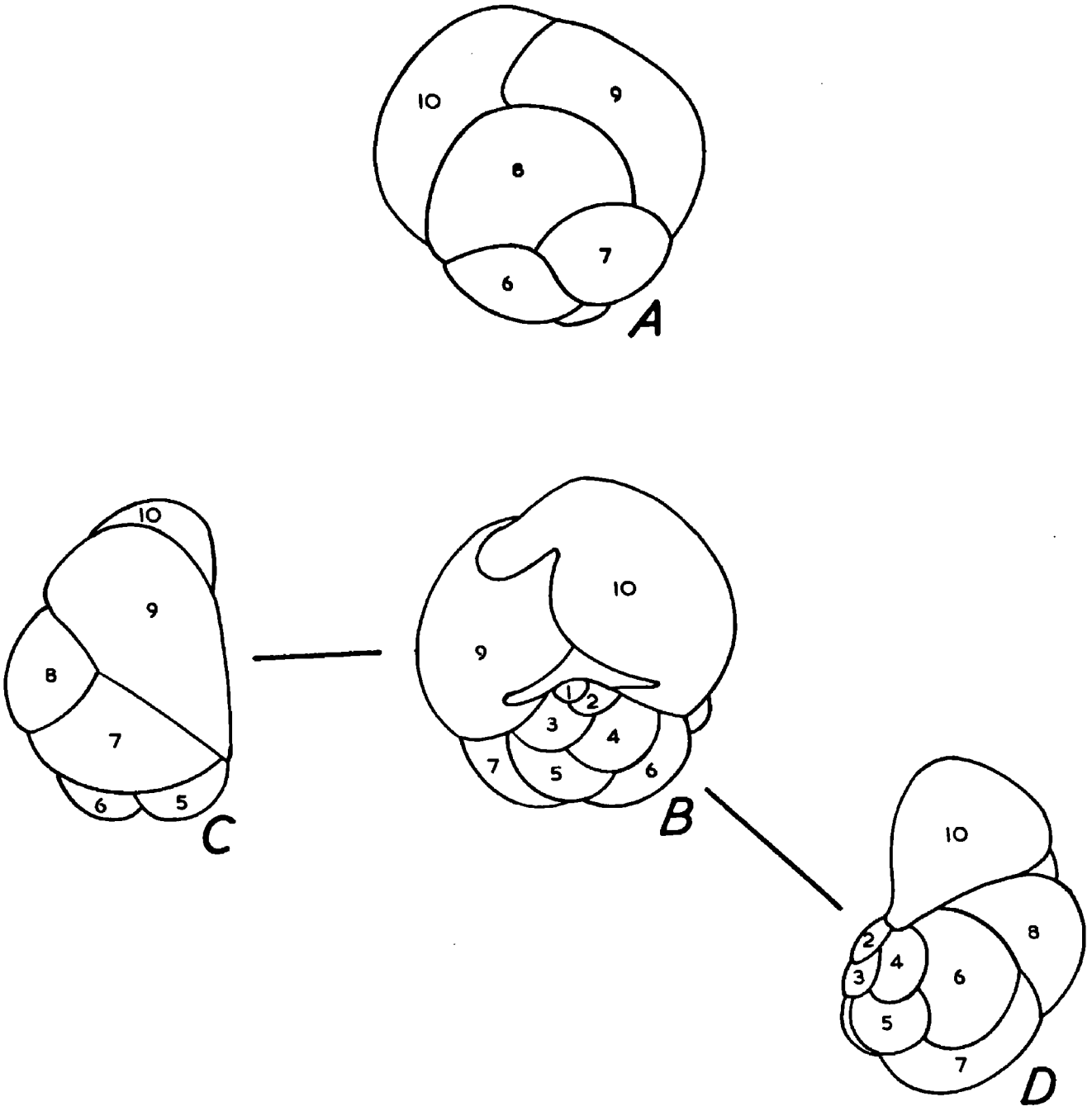
A diagram based on photographs of the Lectotype (cf. Plate 24, figs.9-11) to show the form and arrangement of the chambers.

A. dorsal view.

B. ventral or apertural view.

C. lateral view.

D. oblique lateral view.


10
9
8
7
6
A
10
9
8
7
6
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C
10
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D

unfounded. Examination of sections of Globivalvulina bulloides in the plane of biseriality (sagittal section) and at right angles to this plane (axial section) shows that some recently described species must be regarded as synonyms since they are based on characters which are broadly controlled by the attitude of the section. Reitlinger differentiated G. kamensis from G. bulloides by its more rapidly expanding spiral, but this was pure supposition, and the sagittal sections are virtually identical. Similarly, G. minima differs only in that it has slightly fewer chambers and is in a more excentric sagittal section. The presence of a septal lamellae, which was emphasised by Reitlinger (1950 p.78), has no particular diagnositc value since it depends on the attitude of the section in relation to the valvular projection of the penultimate chamber.

The manner in which the last chamber extended across the periphery to break thebiserial series was the diagnostic feature of G. ovata according to Cushman & Waters, (1928 and 1930). Clearly this suggestion is based on a misunderstanding of the structure of the genus, and it is a feature which results simply from the rapid expansion of the chambers together with shallowly trochoid nature of the spiral (cf. Text fig.15). There does not seem to be any external feature which would separate this species from G. bulloides,

indeed, study of Brady's syntypes suggests that G. ovata is closer to Brady's specimens than G. bulloides of Cushman & Waters (1928 and 1930).

Preservation and Matrix:

Globivalvulina bulloides is morphologically identical to G. parva and these species would be regarded as synonyms if only external morphology was considered. Examination of the wall structure, however, shows that at any given diameter the wall of G. bulloides is approximately twice as thick as that of G. parva. The wall of G. bulloides is rather coarsely granular and commonly shows definite evidence of radiate structure, although in the early chambers the wall has a more homogeneous structure. On the other hand the wall of G. parva is thin dark, homogeneous, and rarely show evidence of radiate structure. Furthermore, it is apparent that this difference cannot by attributed to diagenetic causes for the contrast in the walls is not related to the presence or absence of the radiate layers alone but to the thickness of the basic granular layers.

The possibility of an ecological control of the wall thickness can not be overlooked, (Hendrix, 1958), but in the face of almost complete lack of information on this topic and the apparent progressive increase in

thickness of the globivalvulinid wall in time, it is regarded, for the moment, as a valid taxonomic criterion.

Horizon and Facies:

The material described originally by Brady would appear to be from an Upper Pennsylvanian or Lower Permian horizon although its exact location is not now known. Similar material from Texas (Cushman & Waters, 1928 and 1930, and Plummer, 1945) suggests that the species had a range of this type. It was suggested by de Civrieux (1951) that G. bulloides was confined to strata of Lower Pennsylvanian age, but the evidence, born out in the records of Reitlinger (1950), is that the species has a more extensive range.

GLOBIVALVULINA PARVA Chernysheva, 1948.

Plate 25, Figs.3-12.

Globivalvulina parva Chernysheva, 1948, p.249, Plate XVIII, figs.1-4.

Globivalvulina moderata Reitlinger, 1949, p.158, fig.4a,b.

Globivalvulina scaphoidea Reitlinger, 1949, p.159, fig.5.

Description:

Test free, small, hemispherical, consisting of five or six pairs of biserially arranged chambers in a shallow helical spire of about one and a half whorls; chambers broad, inflated, rapidly expanding in size, slightly compressed dorso-ventrally with flat to concave apertural face; sutures distinct, depressed; wall thin, dark, finely granular, sometimes showing very slight evidence of radiate structure; aperture low, slitlike, on terminal face of the last chamber with distinct valvular projection extending across the opposed aperture and valvular projection of penultimate chamber; septa flat to concave, slightly thicker at apertural end; proloculum spherical.

Dimensions:

Specimen No.	Diameter Apertural Face	Diam. Spire	Height Spire	Height Last Chamber	No. Chambers	Thickness of Wall.
P.420/1	-	0.36	-	0.17	9	0.009
P.420/2	0.31	0.31	-	0.13	-	0.010
P.420/3	0.37	0.32	-	0.14	-	0.013
P.420/4	-	0.15	0.11	0.077	5	0.005
P.420/5	-	0.31	-	-	-	0.014
P.420/6	-	0.25	-	-	-	0.009
P.420/7	-	0.28	-	-	-	0.009
P.420/8	0.35	0.31	-	-	-	0.007
P.423	0.25	0.26	-	-	-	0.007

Depository:

Hunterian Museum of the University of Glasgow, Specimen Nos.P.420/1-8, from Castlecary Limestone, Westerwood Quarry, near Castlecary, Dunbartonshire, and Specimen No.P.423, from Castlecary Limestone, Bowdenhill Quarry and mines, Bowdenhill, Linlithgowshire.

Comparison and Affinities:

The very diminutive species Globivalvulina parva is based principally on sections parallel to the axis of biseriality (Chernysheva, 1948, Plate 18, figs.1,3 and 4) which cut only a single rank of the biserially arranged chambers. These sections are closely similar to the present material when cut in a comparable plane

of section (cf. Plate 25, figs.3 and 6). The single section tangent to the dorsal surface (Chernysheva, 1948, Plate 18, fig.2) is not in itself diagnostic but it is almost identical to sections (Plate 25, figs.4 and 12) of material from the Upper Limestone Group. Thus, although the characters of G. parva are rather inadequately given, it does not appear to differ significantly from the Scottish material.

The species G. moderata and G. schaphoidea described by Reitlinger (1949) are based largely on sections in the plane of coiling and biseriality, hitherto unknown in G. parva. The differentiation of the three species is based mainly on the dimensions together with variations in chamber form and test shape, which are related fundamentally to the manner in which the plane of section intersects the test. Examination of a more comprehensive range of sections from a single horizon within the Upper Limestone Group suggests that they should be regarded as synonyms. G. scaphoidea was distinguished from the other species by means of its small dimensions and its apparent character of having a distinctly inflated final chamber. Reitlinger (1949 p.159) took this specimen to represent a single rank of eight or nine chambers, whereas, the section is, in its early part, in the overlapping biserial part of the test, passing in the later stages

into a single chamber because of the trochoid nature of the coiling. The dimensions of the test are quite normal for a specimen with a total of eight chambers (four in each rank), and do not differ from those of G. moderata with the same number of chambers.

The characters of this species, as they have been defined here, are very closely similar to Gl. bulloides, and, indeed, the two species appear to differ only in the character of their walls, as has been discussed above.

Preservation and Matrix:

This species as described by Chernysheva (1948) sometimes shows evidence of a radiate layer in the wall. The material from the Upper Limestone Group is from limestones which are extensively recrystallised and dolomitised, and, most typically, they display a thin, dark, finely granular, apparently homogeneous wall. A single specimen has been observed in which some evidence of radiate structure can be seen, (Plate 25, fig.11) and while the wall of this specimen is slightly thicker than average, nevertheless, it is thinner than the wall in G. bulloides in specimens of equivalent size.

Horizon and Facies:

First recorded from the upper part of the Lower Carboniferous in the U.S.S.R. by Chernysheva (1948)

and apparently extending throughout the Middle Carboniferous, (Reitlinger, 1949 and 1950), G. parva is now recorded for the first time in Scotland where it occurs sporadically throughout the Castlecary Limestone. It is most abundant in the richly algal, argillaceous, lower part of this horizon, which marks the top of the Upper Limestone Group.

GLOBIVALVULINA GLOBULUS sp. nov.

Plate 25, Figs.13-19.

Description:

Test free, small globular, consisting of not more than five pairs biserially arranged chambers in a rapidly expanding trochoid spire of about one whorl; chambers inflated, globular, rapidly expanding in size, not strongly overlapping, typically eight in number, four in each rank; sutures distinct, depressed; wall thin, dark, finely granular; aperture simple, basal, semi-circular, without pronounced valvular projection; septa convex, maintaining curve of the chamber, not flattening in region of aperture, with thickened end forming apertural lip; proloculum globular.

Dimensions:

Holotype, P.421/1:

Diameter of Spire - 0.19 mm.

Height of last chamber - 0.08 mm.

Height of aperture - 0.03 mm.

Diameter of proloculum - 0.03 mm.

Thickness of wall in last chamber - 0.009 mm.

Specimen No.	Diameter Apertural Face(mm.)	Diam. Spire (mm.)	Height Last Chamber (mm.)	Diam. Prol. (mm.)	No. Chambers in Test.
P.421/2	-	0.25	-	-	-
P.422/7	0.25	0.20	0.08	-	-
P.422/8	0.20	0.18	0.08	-	-
P.422/9	0.20	0.23	-	-	-
P.422/10	-	0.24	-	-	-
P.422/11	0.24	0.25	-	-	-
P.422/1	0.20	0.18	-	0.030	8
P.422/2	0.20	0.19	-	0.034	8
P.422/3	0.24	0.26	0.10	0.034	9
P.422/4	-	0.18	-	-	7
P.422/5	0.16	0.14	-	0.027	6
P.422/6	-	0.23	-	0.030	8

Depository:

Hunterian Museum of University of Glasgow on slide Nos.P.421/1-2 from Index Limestone, Kennox Water, near Douglas, Lanarkshire, and specimens Nos.P.422/1-11 from Index Limestone, Poneil Water, Coalburn, Lanarkshire.

Comparison and Affinities:

This species with its inflated globose chambers and trochoid spiral closely resembles Globivalvulina bulloides Brady, however, careful investigation of

specimens in limestone plates shows that the aperture is a simple high lunate or semi-circular slit without the valvular projection of G. bulloides. Furthermore, the apertural face of this form is consistently convex, so that in its apertural character it resembles Palaeotextularia. It is, therefore, considered that in its generally smaller dimensions and distinct apertural characters, this species can be differentiated from G. bulloides and other species of this genus.

Preservation & Matrix:

Most of the material examined is from limestones which have been recrystallised and replaced by dolomite to a varying degree, but, it is probable that despite the alteration of the matrix the single layered granular wall represents the original structure of the test. No evidence has been found of the hyaline layers described by Reichel (1945 p.550) and others, and, although Cummings (1956 p.209) has shown that such layers may be lost through recrystallisation in the palaeotextulariids, this mechanism is not believed to have operated in this instance, for 'fibrous' layers are preserved in the palaeotextulariids and other genera.

Horizon & Facies:

Globivalvulina globulus has been recorded from the Index, Lyoncross and Orchard limestones, the lower part of the Upper Limestone Group of the Scottish Namurian. It is most abundant in the clean bioclastic limestone facies and it is rare in the more argillaceous limestones. It has not yet been recorded from the calcareous shale facies.

Sub-Order	TEXTULARIINA	Delage & Herouard, 1896.
Superfamily	LITUOLACEA	de Blainville, 1825.
Family	TROCHAMMINIDAE	Schwager, 1877.
Subfamily	TROCHAMMININAE	Schwager, 1877.
Genus	TROCHAMMINA	Parker & Jones, 1859.

TROCHAMMINA SCOTICA sp. nov.

Plate 26, Figs.1-17.

Description:

Test small, free, trochoid, umbilicate, with up to four whorls, each with 6 or 7 chambers, all whorls visible on convex dorsal side, only those of the last whorl on the concave ventral side; chambers uniformly increasing in size, triangular in ventral view, broadly rounded, peripherally tapering towards umbilicus, with gently convex ventral surface; sutures slightly depressed, radial on the ventral surface, curving into periphery on dorsal surface; periphery faintly lobulate; aperture ventral, semi-circular on the inner margin of the chamber close to the umbilicus; wall agglutinate, calcareous-ferrugenous cement.

Dimensions:

Whorl No.	Prol.	1	2	3	Last.
P.424/1.-					
Diam.	0.026	0.11	-	-	-
Height	-	0.077	-	-	-
P.424/2 -					
Diam.	0.034	0.14	0.21	-	-
Height	-	0.085	0.13	-	-
P.424/3 -					
Diam.	-	0.10	0.22	0.31	-

Whorl No.	Prol.	1	2	3	Last.
P.424/3.-					
Height	-	0.068	0.14	0.21	-
P.424/4.-					
Diam.	-	1+ whorls.	6 chambers	-	0.11
Height.	-	-	-	-	-
P.424/5.-					
Diam.	0.026	0.13	0.23	-	-
Height	-	0.068	0.15	-	-
P.424/6.-					
Diam.	0.026	0.10	0.17	0.26	-
Height.	-	0.057	0.10	0.21	-
P.424/7.-					
Diam.	-	1+ whorls	6 chambers		0.16
Height	-	-	-	-	-
P.424/8.-					
Diam.	0.026	0.14	6 chambers	-	-
Height.	-	-	-	-	-
P.424/9.-					
Diam.	0.021	0.11	0.22	0.30	-
Height	-	0.060	0.10	0.18	-
P.424/10.-					
Diam.		1+ whorls	7 chambers		0.18
Height	-	-	-	-	-

Whorl No.	Prol.	1	2	3	Last.
P.424/11.-					
Diam.	0.030	0.10	0.18	-	-
Height	-	0.068	0.13	-	-
P.424/12.-					
Diam.	0.042	with 4 chambers			0.15
Height	-	-	-	-	-
P.424/13.-					
Diam.	-	2+ whorls	7 chambers		0.27
Height	-	-	-	-	-
P.424/14.-					
Diam.	0.038	0.13	0.21	-	-
Height	-	0.085	0.15	-	-
P.424/15.-					
Diam.	0.030	0.094	0.18	0.25	0.32
Height	-	0.060	0.10	0.15	0.23
P.424/16.-					
Diam.	0.030	0.10	0.17	0.25	0.34
Height	-	0.051	0.11	0.14	0.23

Depository:

Hunterian Museum of the University of Glasgow, P.424/2 Holotype and P.424/1 & 3-16, from Castlecary Limestone, Westerwood Quarry, near Castlecary, Dunbartonshire, Scotland.

Comparison & Affinities:

Few Carboniferous species of this genus have been described, and Trochammina scotica is distinctive both in the height of its spire and in having six to seven chambers in a whorl.

Preservation & Matrix:

Although the limestone in which this species is preserved is consistently dolomitised and recrystallised, it is believed that the majority of the coarse angular fragments in the wall are original agglutinate particles, and not secondary crystalline material resulting from grain growth (Cummings, 1956 p.209). Confirmation of this is to be found in the fact that a number of the particles show distinct fibrous, or lamellar organic structure, while some specimens include small spherical bodies in the wall which may be calcisphaera or prolocula of other species. The host sediment is also quite extensively pyritised, and the pyrite is consist-:ently associated with organic debris where it occurs as fine dust and very small granular particles, which may form clot-like aggregates. The test of T. scotica is quite selectively affected by this replacement and this is attributed to the probable organic basis of its agglutinate wall (Hedley, 1963).

Horizon & Facies:

This species is known so far only from the richly algal, slightly argillaceous, lower part of the Castlecary Limestone, the uppermost limestone of the Upper Limestone Group of the Scottish Namurian.

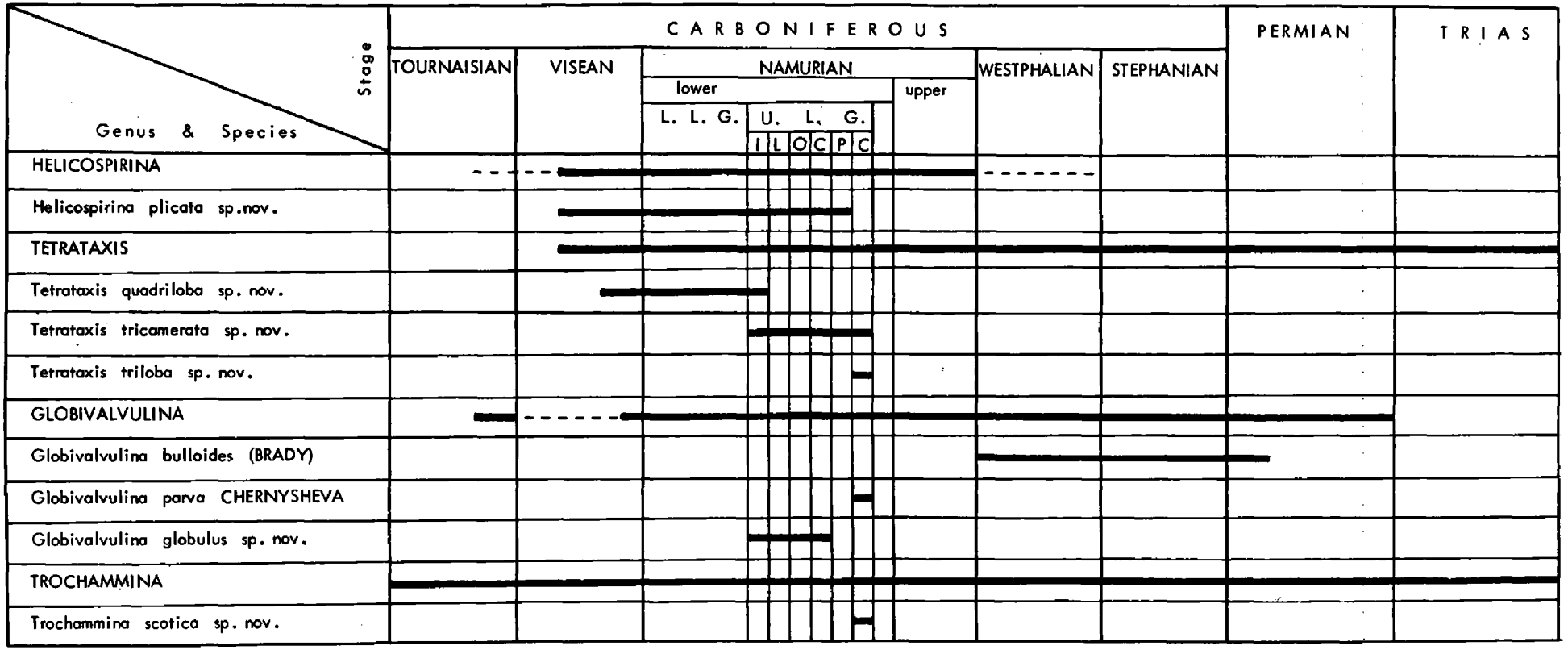
STRATIGRAPHIC DISTRIBUTION.

The distribution of Helicospirina and the associated genera discussed above is shown in Text-figure 16. This table indicates the absolute range of the genera, so far as is known from present records, in the Upper Palaeozoic.

The distribution of species is similarly illustrated but, in this case, the information is based largely on their occurrence in Britain, and is given with particular reference to the Upper Limestone Group of the Scottish Carboniferous.

TEXT - FIGURE 16.

Chart summarising the distribution of the genera and species discussed in Chapter 4. The ranges of the species are shown with particular reference to the Upper Limestone Group (U.L.G.) in which the principal marine horizons are indicated by their initial capital letter.


Stage
Genus & Species
CARBONIFEROUS
PERMIAN
TRIAS
TOURNAISIAN
VISEAN
NAMURIAN
lower
upper
L. L. G.
U. L. G.
I L O C P C
WESTPHALIAN
STEPHANIAN
HELICOSPIRINA
Helicospirina plicata sp.nov.
TETRATAXIS
Tetrataxis quadriloba sp. nov.
Tetrataxis tricamerata sp. nov.
Tetrataxis triloba sp. nov.
GLOBIVALVULINA
Globivalvulina bulloides (BRADY)
Globivalvulina parva CHERNYSHEVA
Globivalvulina globulus sp. nov.
TROCHAMMINA
Trochammina scotica sp. nov.

EXPLANATION OF PLATE 22.

1-7. *Helicospirina plicata* (Brady).

1. axial section showing tubular umbilical cavity and adjacent apertural opening. X200. (cf.Text fig. 10E). P.503/1.
2. parallel axial section. X200. (cf. Text fig.10F). P.503/2.

Both from Lyoncross Limestone, Craigburn, Uddington.

3. sagittal section showing cross-section of umbilical cavity and radially arranged septa. X200. (cf. Text fig.10A), P.504;

From Lyoncross Limestone, Garpel Water, Muirkirk.

4. oblique section. X200. (cf. Text fig.10C), P.503/3;
5. sagittal section. X100. P.505;

Both from Lyoncross Limestone, Craigburn, Uddington.

6. parallel axial section tangential to tubular umbilicus and showing apertural pores adjacent to umbilicus. X100. B.M.N.H. P.45501;
7. sagittal section, B.M.N.H. P.45500;

Both from shales over top Hosie Limestone, Brankumhall Quarries, East Kilbride.

PLATE 22. - cont.

8-12. Tetrataxis quadriloba sp. nov.

8. axial section showing thick fibrous buttresses overlapping sub-tubular valvular projections in the umbilical cavity. X50. P.79/3; (John Young Collection).

9. sagittal section showing four chambers in whorl. X50. P.79/2; (John Young Collection).

10. sagittal section near apex of test showing four chambers in whorl. X50. P.79/1; (John Young Collection).

11. axial section showing balanced arrange-:ment of chambers on right and left of spire. X50. P.79/4; (John Young Collection).

12. same as fig. 10 X100.


1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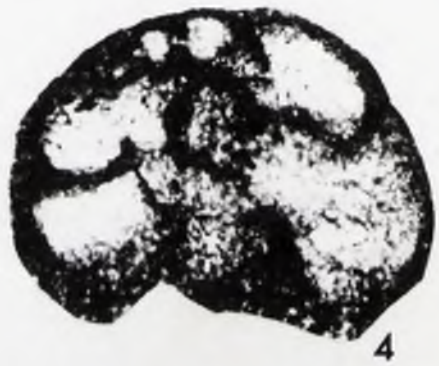
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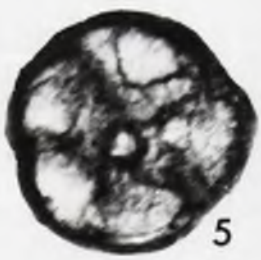
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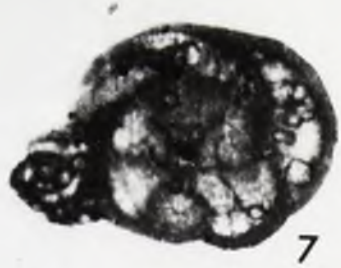
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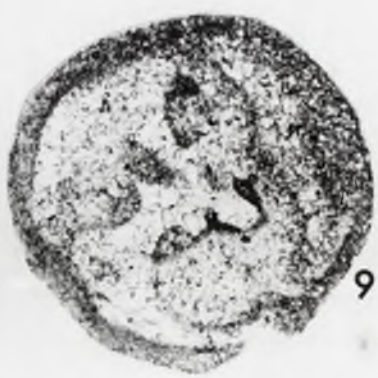
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EXPLANATION OF PLATE 23.

1-4,6. *Tetrataxis tricamerata* sp. nov.

1. axial section showing overlapping tubular projections in umbilical cavity. X50. P.427/1;

Shale parting in Orchard Limestone, Craigburn, Uddington.

2. sagittal section showing three chambers in a whorl. X100. P.426/1.

3. as fig.2 X50.

From shales over Lyoncross Limestone, Whitecraigs, Renfrewshire.

4. sagittal section..X50. P.429; Castlecary Limestone, Westerwood Quarry.

6. sagittal section showing complex umbilical cavity subdivided by overlapping subtubular projections of the chambers. X50. P.506;

Orchard Limestone, Putyan Burn, Dalry.

5,7-14. *Tetrataxis triloba* sp. nov.

5. axial section showing very slender wall without fibrous buttresses and complex umbilical cavity. X50. P.430/1;

7. as fig.5. X100.

8. axial section. X100. P.430/3.

PLATE 23. - cont.

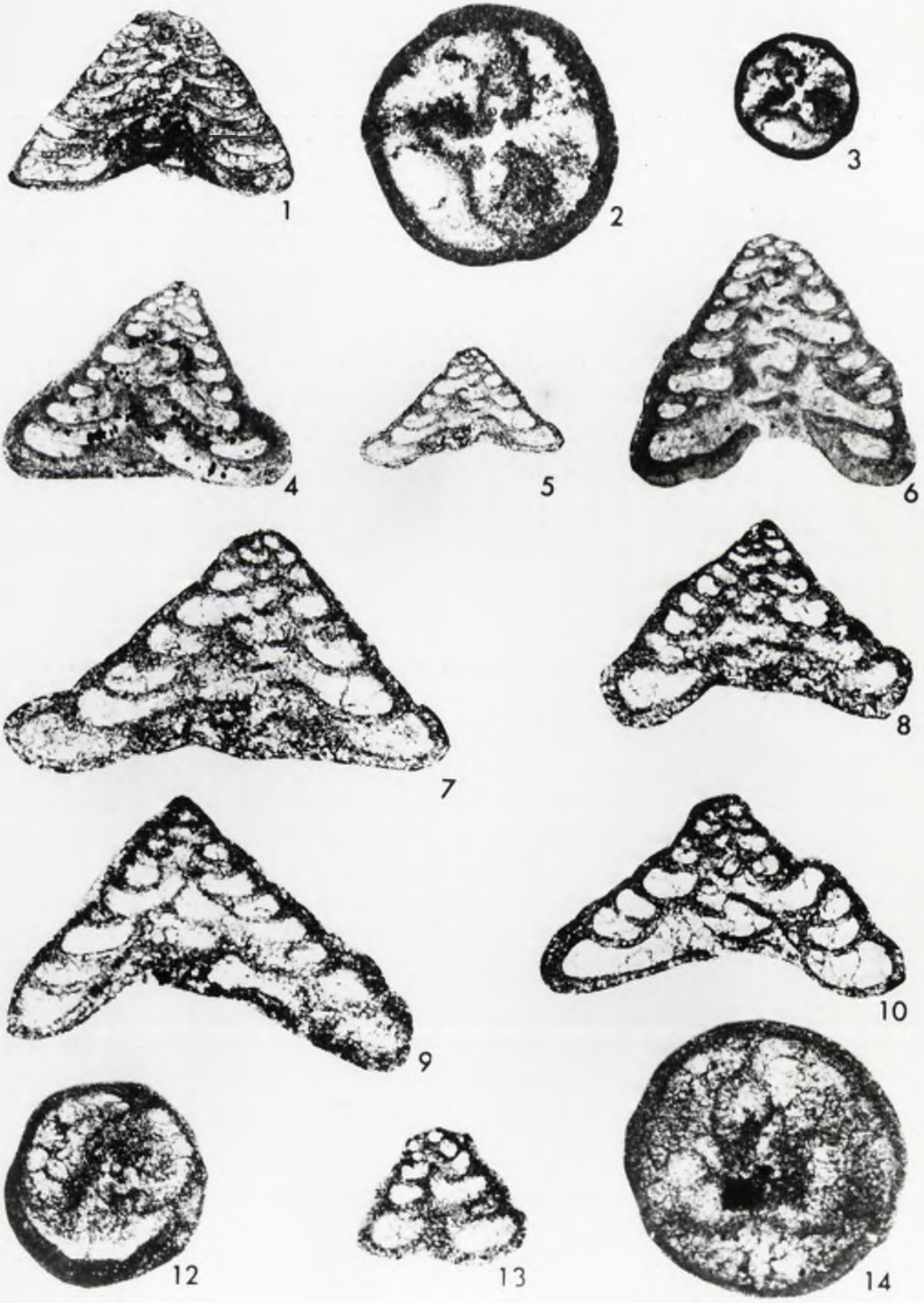
9. oblique section showing collapse of chambers into umbilical cavity. X100. P.430/5.

10. oblique axial section showing compression of the apical part of the test into the lower chambers. X100. P.430/2.

12,14 sagittal sections showing the chambers arranged three in a whorl. X100. P.430/6, P.430/7.

13. oblique axial section of the apical part of test showing the proloculum and initial chambers. X100. P.430/4.

All from Castlecary Limestone, Westerwood Quarry.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EXPLANATION OF PLATE 24.

1-4. *Tetrataxis tricamerata* sp. nov.

1,3. lateral views showing the arrangement of the chambers (cf. Text fig.14) X50.

2. dorsal view showing the arrangement of three chambers in a whorl at the apical part of the test. X50.

4. ventral view showing three chambers. X50.

HOLOTYPE P.425, Orchard Limestone, Poniel Water, Coalburn.

5-11. *Globivalvulina bulloides* (Brady).

5. apertural view showing valvular projection of last chamber and umbilical depression.

6. lateral view.

7. dorsal view.

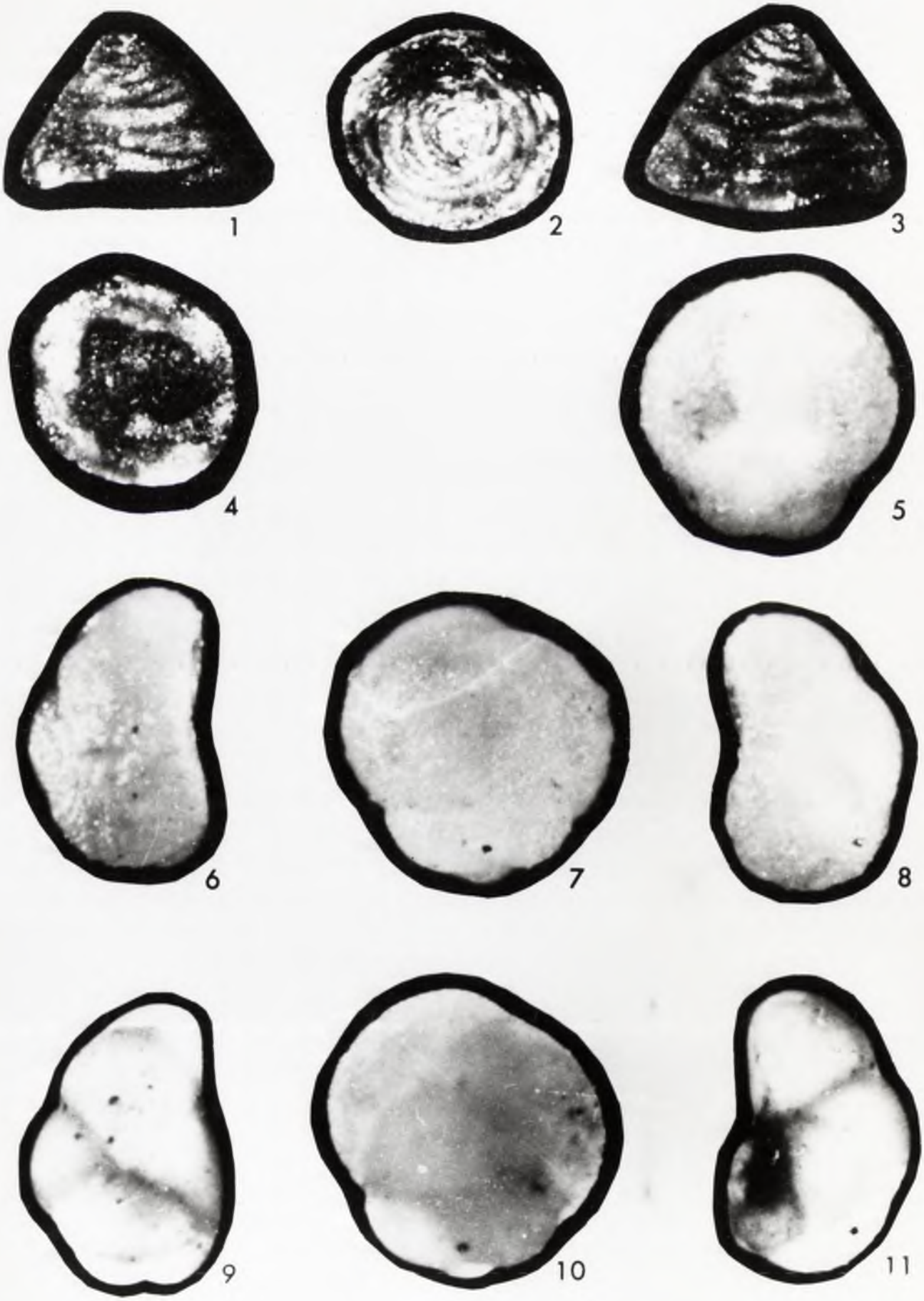
8. lateral view.

9. same lateral view as fig.6, but with light refracted through the specimen showing chamber arrangement. (cf. Text fig.15).

10. dorsal view in refracted light.

11. lateral view in refracted light. (cf. Text fig.15).

All X100. LECTOTYPE, B.M.N.H. P.41652; Fusulina-beds, Upper Coal Measures, Iowa.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EXPLANATION OF PLATE 25.

All figures X100.

1,2. Globivalvulina bulloides (Brady).

1. section parallel to apertural face showing umbilical cavity, and the position of the valvular projections; PARALECTOTYPE, B.M.N.H. P.45679.

2. sagittal section showing proloculum and biserial overlap of chambers. Note the thick wall; PARALECTOTYPE, B.M.N.H. P.45678 from Fusulina-beds, Upper Coal Measures, Iowa.

3-.2 Globivalvulina parva Chernysheva.

3. parallel sagittal section showing only a single rank of chambers, P.420/1;

4. section cutting dorsal part, P.420/2;

5. axial section, P.420/3;

6. juvenile showing proloculum and 5 chambers - 3 clearly visible, P.420/4;

7. oblique section, P.420/5;

8,9. sections slightly oblique to dorsal surface P.420/6 and P.420/7;

10. section tangential to ventral, or apertural face, showing valvular projections and umbilical space, P.420/8;

PLATE 25. - cont.

11. section showing evidence of fibrous structure in wall, P.420/9;

All from Casltecary Limestone, Westerwood Quarry.

12. section of dorsal surface, P.423;

from Castlecary Limestone, Bowdenhill Quarry & Mines.

13-19. Globivalvulina globulus sp. nov.

13. sagittal section showing globose chambers, biserial overlaps and simple aperture, HOLOTYPE P.421/1;

14. section of dorsal surface, P.422/7;

15. oblique section showing globose chambers, P.422/10;

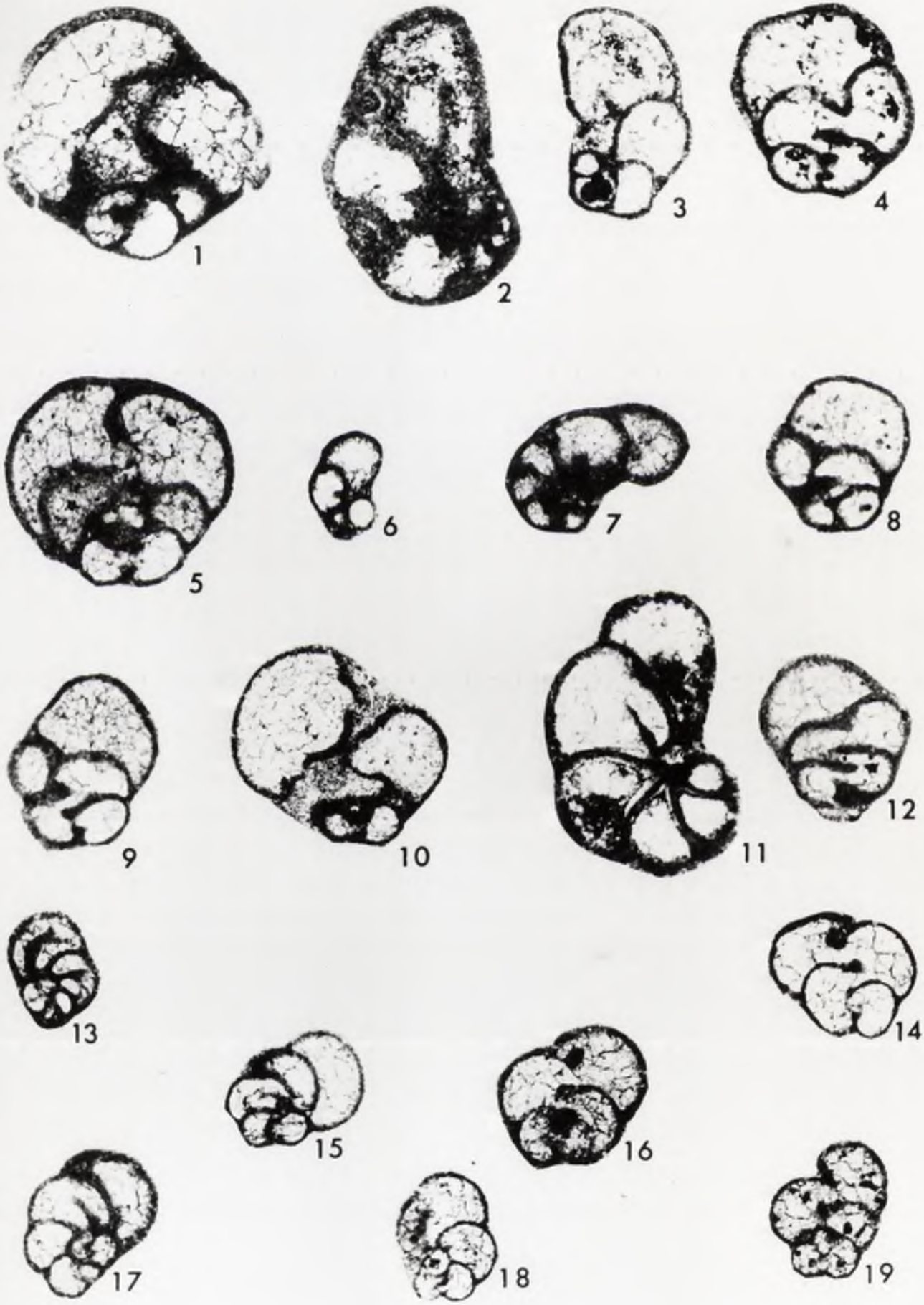
16. section of dorsal surface, P.422/11;

17. oblique section, P.421/2;

18. oblique section, P.422/8;

19. axial section, P.422/9;

All from Index Limestone. (13 & 17) from Kennox Water and (14-16 & 18-19) from Poniel Water, Coalburn.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EXPLANATION OF PLATE 26.

All figures X100 unless stated otherwise.

1-17. *Trochammina scotica* sp. nov.

1. axial section showing proloculum, tubular umbilicus, with adjacent apertural openings. Note small fragments of agglutinate organic material in the wall which is heavily pyritised. X300. HOLOTYPE P.424/2;
2. as fig. 1;
3. axial section slightly oblique, P.424/6;
4,5. sagittal sections showing trochospiral arrangement of the chambers, P.424/10 & P.424/8;
6. oblique axial section, P.424/9;
7. sagittal section showing dark umbilical zone with radial septa and aperture adjacent to umbilicus, P.427/17;
8. sagittal section showing proloculum and first four chambers, p.424/12;
9. sagittal section showing seven chambers, P.424/13;
10,11 oblique sections, P.424/14 & 15;
12. parallel axial section, P.424/18;
13, section parallel to lateral slope of the test, P.424/19;

PLATE 26. - cont.

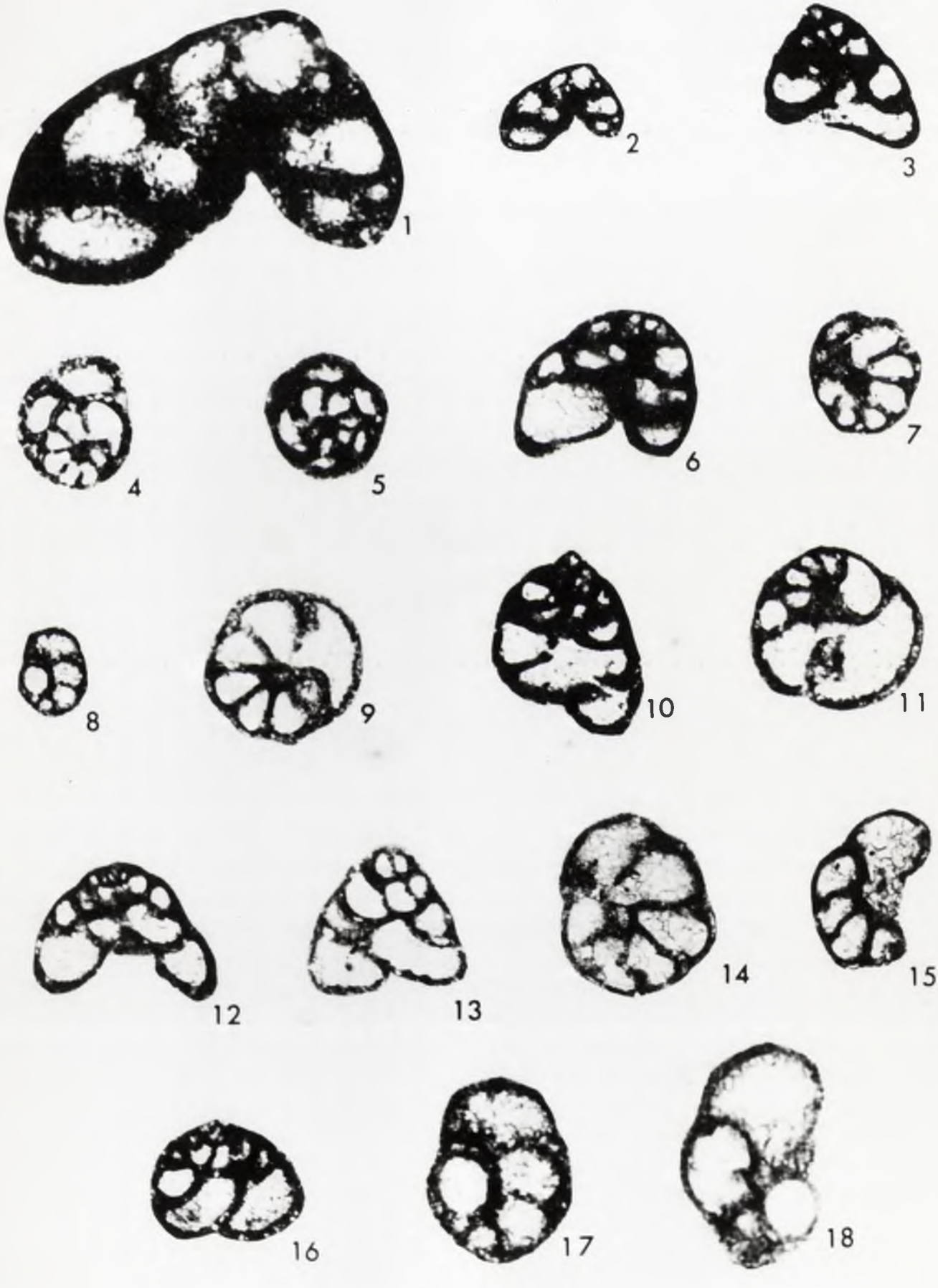
14. sagittal section showing central hollow umbilicus with radial septa, P.424/20;

15. oblique section tangential to ventral surface. This section shows superficial resemblance to Globivalvulina (cf. fig.18) P.424/21.

16. oblique section, P.424/22;

17,18. comparison of fig.8 X200 and Globivalvulina Plate 25, fig.6. X200, to illustrate difference in form and arrangement of the chambers.

All from Castlecary Limestone, Westerwood Quarry.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CHAPTER 5.

The Foraminifera and their Stratigraphical Significance.

- oOo -

The application of smaller foraminifers in Upper Palaeozoic stratigraphy was discussed in detail by Cummings (1958), who suggested a technique which integrated three traditionally applied, but normally independant, methods of study. The salient steps of this technique are: (Cummings, 1958 p.21):

1. Analysis of assemblages from friable rock material by population studies etc., leading to systematic identification.
2. Serial sectioning of norms and end members of scatters within the assemblages.
3. Analysis of hard rock faunas by microscopic examination of the sections, with recognition of
   a) inherent limitations;
   b) the integrative effect of comparison with results of the serial sectioning;
   c) the pattern of the bioseries;
   d) the partial systematic identification.
4. Summarising of the results of the analyses made in steps (1) and (3), by;
   a) range charts showing the absolute distribution of genera and species;
   b) diagrammatic charts showing the outline morphogeny and/or phylogeny;

c) quantitative distribution charts
of each particular group.

Such a comprehensive treatment is time consuming, and, although profitable in the accuracy of its results, is commonly impracticable because of the difficulty or impossibility of obtaining solid specimens.

Because of the scarcity of free specimens Cummings (1961 p.108) suggested some modification in his integrated technique (Cummings, 1958), although still reiterating that specific identification of randomly cut sections is impossible except where closely adjacent horizons provide assemblages of solid specimens for population studies. In the modified procedure Cummings (1961 p.108) relies principally on the recognition of bioseries, and considered the distribut-:ion of families and genera rather than that of individual morphospecies. At the same time an attempt was made to assess the effects of facies, sedimentation, and diagenesis on the patterns of the assemblages, in order that their stratigraphic value may be assessed. A zoning of the British Carboniferous was proposed with two zones in the Tournaisian, six zones in the Visean, corresponding broadly with the Visean zones of the Russian Carboniferous, and two zones in the lower part of the Namurian. A sequence of faunal assemblages was recognised and refered to as F.A.1-10.

The Upper Limestone Group falls within a single zone (F.A.10) and it was supposed that it would be difficult to distinguish the limestones on the basis of their foraminiferal content. In practice each major horizon has proved to have a distinctive foraminiferal assemblage which could be readily recognised. (Text figs.31-36). However, the limestones themselves commonly have a distinctive character and can frequently be recognised solely on lithological grounds. Thus, it is possible that the distinctive suite of foraminiferal assemblages reflect predominantly the contrasting facies of the limestones of the Upper Limestone Group, rather than a progressive phylogenetic modification of the foraminiferal stocks. The question then arises of how far the assemblages are influenced by lithology rather than phylogeny. In other words, are the assemblages of smaller foraminifers no more than lithological markers dominated by the kind of facies in which they are found.

A fossil assemblage, as finally observed, is the product of a number of factors which operate at various times from the development of the original biocenosis until the moment of collection.

1) The phyletic factor - the stage and condition of the phyletic trends of each stock present in the living assemblage.

2) The environmental factor - the nature and extent of the modification of the stocks in the assemblage produced by the ecological conditions they experience.

3) The sedimentological factor - modifications of the assemblages produced during the deposition, sorting and final accumulation of the host sediment.

4) The diagenetic factor - modifications of the assemblages produced during the consolidation and later history of the host sediment.

5) The collection factor - modification of the assemblages produced through bias in the methods of abstraction from the host sediment and in later study.

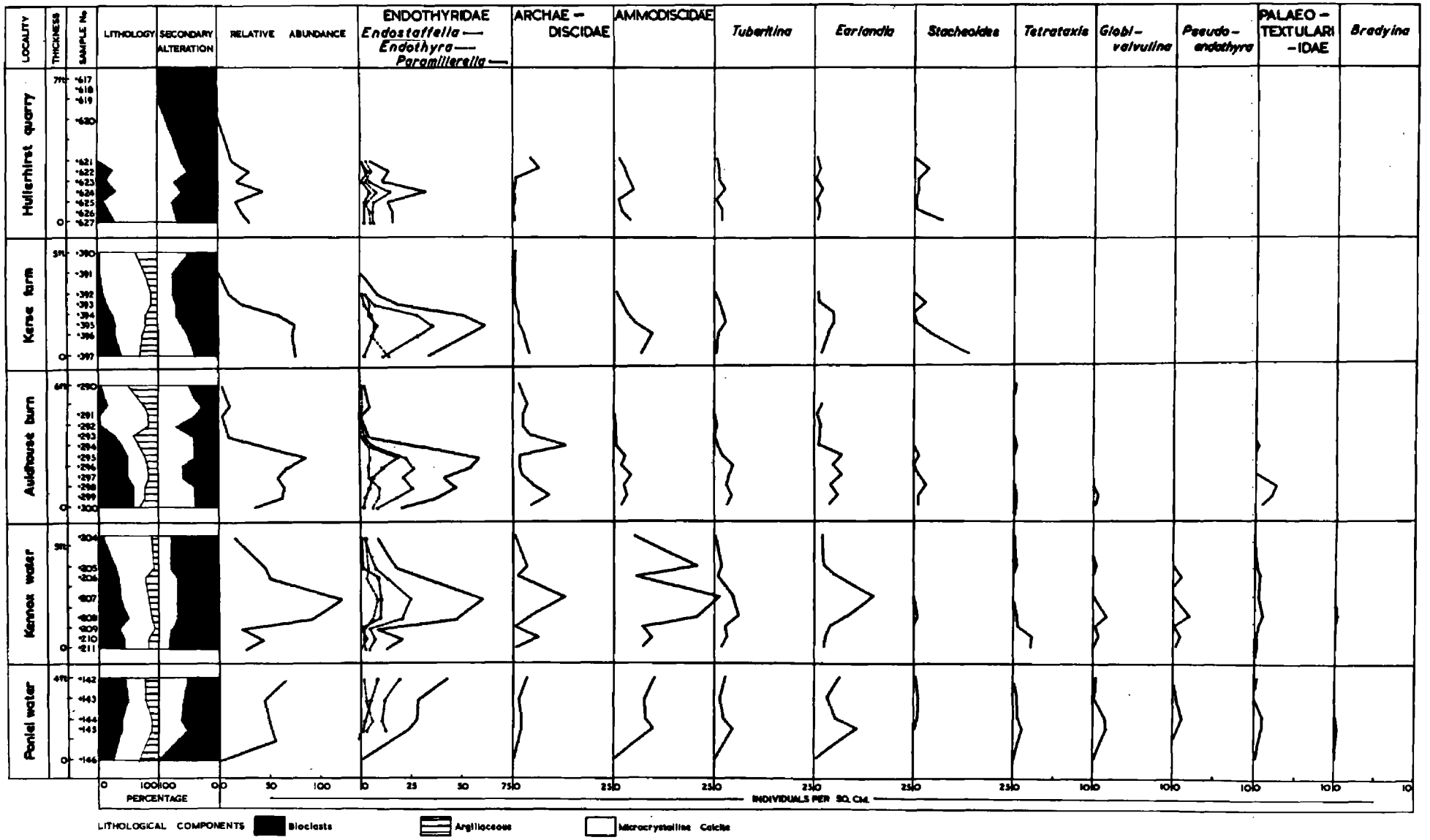
In order to 'isolate' the phyletic factor of an assemblage it is necessary to assess and eliminate, as far as possible, the modifications introduced through the influence of the other factors, for phylogeny is a major criterion of stratigraphic chronology. In attempts to correlate local minor successions the factors of environment etc., have their maximum expression, and a more detailed basis for correlation is required than is achieved by studying the assemblage in terms only of its component families and genera,

particularly where correlation is attempted beyond the confines of a relatively isolated sedimentary basin.

The quantitative distribution of Foraminifera at five localities of the Index Limestone is shown in Text fig.17. The chart demonstrates that the factors controlling foraminiferal abundance are complex, but allows some appraisal of their influence. Thus the cyclical character of sedimentation within the Upper Limestone Group is reflected in the increase in argillaceous content towards top and bottom of the limestone. The dominant marine influence in mid-cycle is reflected in the maximum pulse of foraminiferal abundance at this position. But Text fig.17 also shows that the content of terrigenous material in the limestone is not the only factor influencing foraminiferal abundance, and that the content of foraminiferal tests is related to environment as expressed in content of bioclasts, and to subsequent modification by diagenesis. The control of bioclastic content on the numbers of foraminifers is greatest in relation to benthonic encrusting forms such as Aoujgallia, Stacheoides, Calcivertella, Calcitornella, but other forms such as Tetrataxis also show a strong preference for the more dominantly bioclastic facies (cf. Cummings, 1961 p.110).

TEXT - FIGURE 17.

Quantitative distribution chart of foraminifers at five localities of the Index Limestone. The abundance of the various families and genera is shown in individuals per sq. cm., and this is compared with an assessment of lithology and secondary alteration. The influence of these factors on the populations can be readily observed.


LOCALITY
THICKNESS
SAMPLE No.
LITHOLOGY
SECONDARY ALTERATION
RELATIVE ABUNDANCE
ENDOTHYRIDAE
Endostaffella
Endothyra
Paramillerella
ARCHAE - DISCIDAE
AMMODISCIDAE
Tuberitina
Earlandia
Stacheoides
Tetrataxis
Globi - valvulina
Pseudo - endothyra
PALAEO - TEXTULARI - IDAE
Bradyina
Hullerhirst quarry
Kerse farm
Auldhouse burn
Kennox water
Penkill water
PERCENTAGE
INDIVIDUALS PER SQ. CM.
LITHOLOGICAL COMPONENTS
Bioclasts
Argillaceous
Microcrystalline Calcite

In other instances the factors controlling the abundance of the foraminiferal stocks are not clear. Thus Globivalvulina and the palaeotextulariids are found only when the other foraminiferal groups are at their greatest abundance and occur at only three localities (Text fig.17), and Pseudoendothyra and Bradyina similarly occur at only two localities. The occurrence of these genera may be related to conditions of depth, salinity, or turbidity, which cannot be readily deduced from the lithology of the host sediment. Nevertheless, it may be argued that the palaeotextulariids, Globivalvulina, Pseudoendothyra and Bradyina, since they are associated with the minimum occurrence of terrigenous matter, the maximum occurrence of bioclastic material, and the greatest abundance of foraminifers, represent the period in the sedimentary cycle when the marine phase had its greatest influence. It is apparent that throughout a large part of the Midland Valley the fauna of the Index Limestone is impoverished, for only at the two localities indicated in Text fig.17 has the full range of genera been identified. It is clear that the changes in fauna observed vertically within the lime-:stone reflect the type of change which can be expected as the limestone is traced laterally, and the marine influence decreases progressively towards the east in

the Midland Valley. The appearance of the relatively exotic genera Globivalvulina, Pseudoendothyra and Bradyina in the assemblages of the Index Limestone is controlled by varying ecological conditions associated with cycles of marine transgression and regression. The occurrence of the genera in a restricted facies may give them local value as stratigraphic markers, but for correlation beyond the restricted cyclical framework of the local stratigraphy of the Upper Lime-:stone Group it is necessary to assess their phyletic stage in relation to their probable phylogeny.

Text fig.18 illustrates the quantitative distribution of families, genera, and important species at successive horizons in the Upper Limestone Group. At two horizons striking geographical variation in the assemblages is illustrated showing that, while at some particular horizon and locality the assemblage is characterised by the presence of a particular genus or family, or by its abundance, this rarely has phyletic significance; the population structure and pattern of distribution of groups in the assemblage are predomin-:antly controlled by conditions of environment, sediment-:ation and diagenesis.

In order to provide a more accurate and detailed stratigraphic subdivision than that provided by simple assemblages, it is clearly advantageous to study those

TEXT - FIGURE 18.

Quantitative range chart for the Upper Limestone Group. On the left the distribution of important families and genera is shown, and on the right the distribution of the most important species. At the Lyoncross and Plean horizons a comparison is made between different assemblages which are believed to occur at the same stratigraphic level, although they differ strikingly in character.

NOVELLA
ENDOSTAFFELLA
PARAMILLERELLA
ENDOTHYRA
ARCHAEDISCIDAE
TETRATAXIS
FISCHERINIDAE
PTYCHOCLADIIDAE
PALAEOTEXTULARIIDAE
Endostaffella modica sp. nov.
Endostaffella inflata sp. nov.
Paramillerella indicis sp. nov.
Paramillerella radiata (BRADY)
Paramillerella involuta sp. nov.
Paramillerella craigburnensis sp. nov.
Paramillerella westerwoodensis sp. nov.
Paramillerella gyrensis sp. nov.
Paramillerella hemisphaerica sp. nov.
Pseudoendothyra diaphana sp. nov.
Bradyina perforata sp. nov.
Bradyina pomariformis sp. nov.
Endothyranopsis sphaerica (RAUSER-CHERNOUSSOVA)
Archaediscus cf. grandiculus SCHLYKOVA
Globivalvulina globulus sp. nov.
Globivalvulina parva CHERNYSHEVA
Tuchkammina scotica sp. nov.
Cepekia centrifuga (BRADY)
Earlandia pulchra (CUMMINGS)
Earlandia vulgaris (RAUSER. & REITLINGER)
Tuberitina maljavkini MIKHAILOV
CASTLECARY
Beoch bore
PLEAN
Craigburn
upper
CALMY
lower
ORCHARD
Ayrshire
LYONCROSS
Central area
INDEX
Each division of the scale represents 30% of the total fauna

groups of foraminifers whose distribution is least affected by varying conditions of facies and diagenesis. The members of the Endothyridae shown in Text fig.18, are the group most suited to this task for they occur in greatest numbers and fluctuate least in response to changing conditions of lithology and diagenesis. As Text fig. 18 shows, the genera Paramillerella and Endothyra have the most consistent distribution and so these genera would appear to be most likely to provide a reliable means of stratigraphic discrimination provid-:ing some phylogenetic trend can be established. This obviously demands more detailed study of the biocharacters than is achieved in the consideration of more generalised bioseries of change which provide the basis for the general zonation of the Carboniferous, and some investigation of the range and distribution of species is essential. The objections raised by Cummings (1961 p.108) to specific identification of random sections are largely overcome by the technique of examining foraminifers in indurated limestones as discussed below. (Chapter 2, p.10). Moreover, the procedure adopted enables the changes in the biocharacters of the populations in time to be observed as well as the description of individual species.

1. PARAMILLERELLA.

In the evolution of Paramillerella the test shows progressive increase in the number of chambers, and in the Upper Limestone Group there appears to be a rapid progression in the trend from the more inflated quadrate chamber, in which height and width are approximately equal (Text fig.19, No.35), towards the more rectangular chamber without any appreciable inflation, in which height is greater than width (Text fig.19, No.8). The result of this change in chamber form is that the number of chambers in each whorl of populations of Paramillerella in the Upper Limestone Group are of particular signifi-:cance stratigraphically (Text fig.20). Since the differences in the populations at successive horizons can be established to be statistically significant (Text fig.21), the number of chambers in the test provides an accurate means of stratigraphic discrimin-:ation. Populations in the lower three horizons, (Index to Orchard), have very similar means, and statistical discrimination can be achieved only at minimum levels of significance between adjacent horizons.

Two major lines of morphological development appear to be distinguishable, with a major divergence in the paramillerellid stock possibly occurring during Orchard and Calmy times. In one line, illustrated by the

TEXT - FIGURE 19.

PARAMILLERELLA.

Chart showing the morphogeny of Paramillerella in the Upper Limestone Group. The main trends of phylogeny are indicated by the heavy lines and the ultimate direction of the trends is suggested by the dashed arrows. Pseudoendothyra is included to illustrate that it differs strikingly in detailed morphology from any of the paramillerellid species.

1-6. Paramillerella westerwoodensis sp.nov.

7-8. Paramillerella craigburnensis sp. nov.

9-11. Paramillerella hemisphaerica sp. nov.

13-16, 21-22. P. radiata (Brady).

17-18. P. aff. radiata (Brady).

19-20. P. cf. involuta sp. nov.

23-27. P. ayrensis sp. nov.

28-31. P. indicis subradiata subsp. nov.

34-36. P. indicis indicis subsp. nov.

32-33. Pseudoendothyra diaphana sp. nov.

UPPER LIMESTONE GROUP
CASTLECARY
PLEAN
ORCHARD
LYONCROSS
INDEX
Millerella
Eoschubertella
Staffella
1
2
3
4
5
6
7
8
9
10
11
13
14
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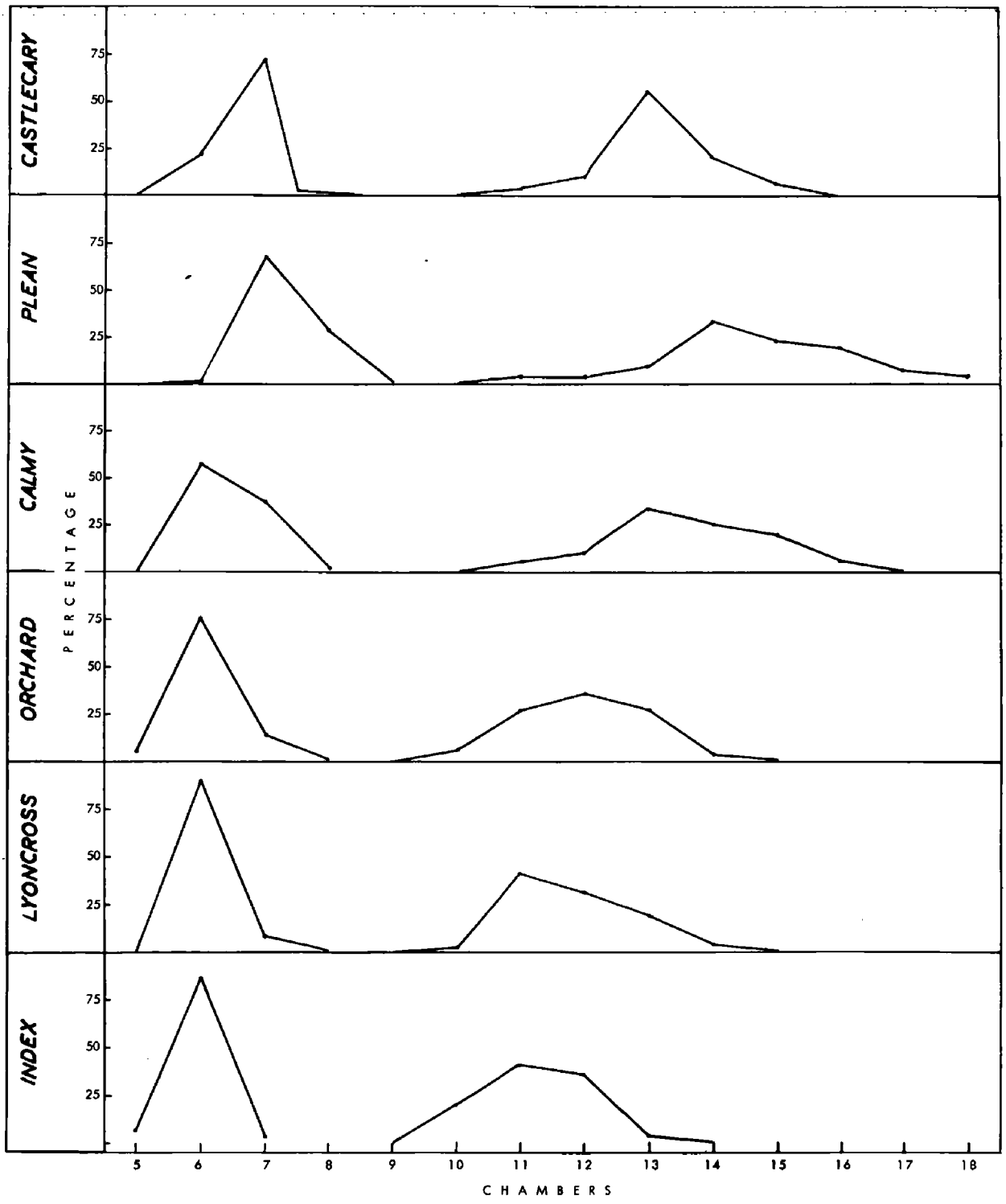
36

TEXT - FIGURE 20.

PARAMILLERELLA.

Chamber frequency in whorls 1 and 3 of populations of species of Paramillerella from successive horizons in the Upper Limestone Group. The modal shift from Orchard Limestone to the Plean Limestone is expressed in the morphogenetic series of Nos.21, 22, 16-20, and 7-8 in Text figure 19, while the smaller shift recorded in the Castlecary Limestone represents the more conservative line of Nos.1-6.


CASTLECARY
PLEAN
CALMY
ORCHARD
LYONCROSS
INDEX
PERCENTAGE
75
50
25
5
6
7
8
9
10
11
12
13
14
15
16
17
18
CHAMBERS

TEXT - FIGURE 21.

PARAMILLERELLA.

The range, standard error of the mean, and mean number of chambers in each half whorl of populations of various species of Paramillerella from a number of horizons and localities in the Upper Limestone Group.

1. Index Limestone, (Paramillerella indicis indicis).

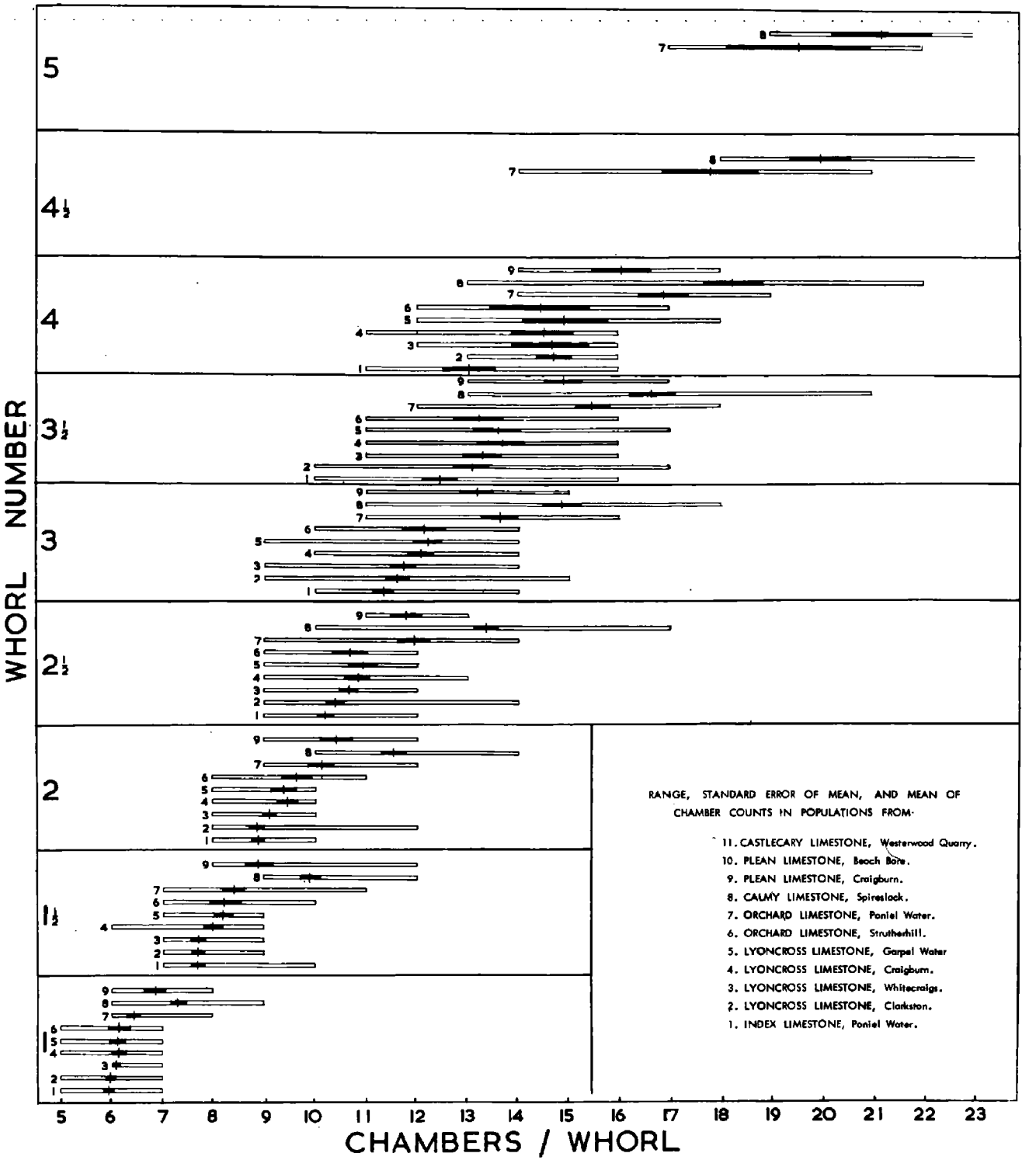
2,3. Lyoncross Limestone. (P. i. subradiata)

4,6. Orchard Limestone, (P. radiata).

7. Calmy Limestone. (P. involuta)

8. Plean Limestone. (P. craigburnensis).

9. Castlecary Limestone. (P. westerwoodensis).


WHORL NUMBER
5
4½
4
3½
3
2½
2
1½
1
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
CHAMBERS / WHORL
RANGE, STANDARD ERROR OF MEAN, AND MEAN OF CHAMBER COUNTS IN POPULATIONS FROM:
11. CASTLECARY LIMESTONE, Westerwood Quarry.
10. PLEAN LIMESTONE, Beach Bore.
9. PLEAN LIMESTONE, Craigburn.
8. CALMY LIMESTONE, Spireslack.
7. ORCHARD LIMESTONE, Poniel Water.
6. ORCHARD LIMESTONE, Struthershill.
5. LYONCROSS LIMESTONE, Garpel Water
4. LYONCROSS LIMESTONE, Craigburn.
3. LYONCROSS LIMESTONE, Whitecraigs.
2. LYONCROSS LIMESTONE, Clarkston.
1. INDEX LIMESTONE, Poniel Water.

morphogenetic series of Nos.21,22, 16-20, 7,8, in Text fig. 19, there is an increase in diameter and form ratio, while in the more conservative line of Nos.1-6 in Text fig. 19, the diameter and chamber counts increase more slowly while the form ratio decreases, leading to forms which are probably ancestral to Millerella. The expansion in size and axial length observed in the more advanced group suggests that the line may be ancestral to such genera as Pseudostaffella and Eoschubertella.

The variation in the diameter of successive whorls in populations of Paramillerella is summarised in Text fig.22, which shows that there is a progressive and statistically significant decrease in diameter per whorl from the Index to the Orchard horizons, and then an increase in diameter which is most striking in the line producing the large forms of the Plean horizon.

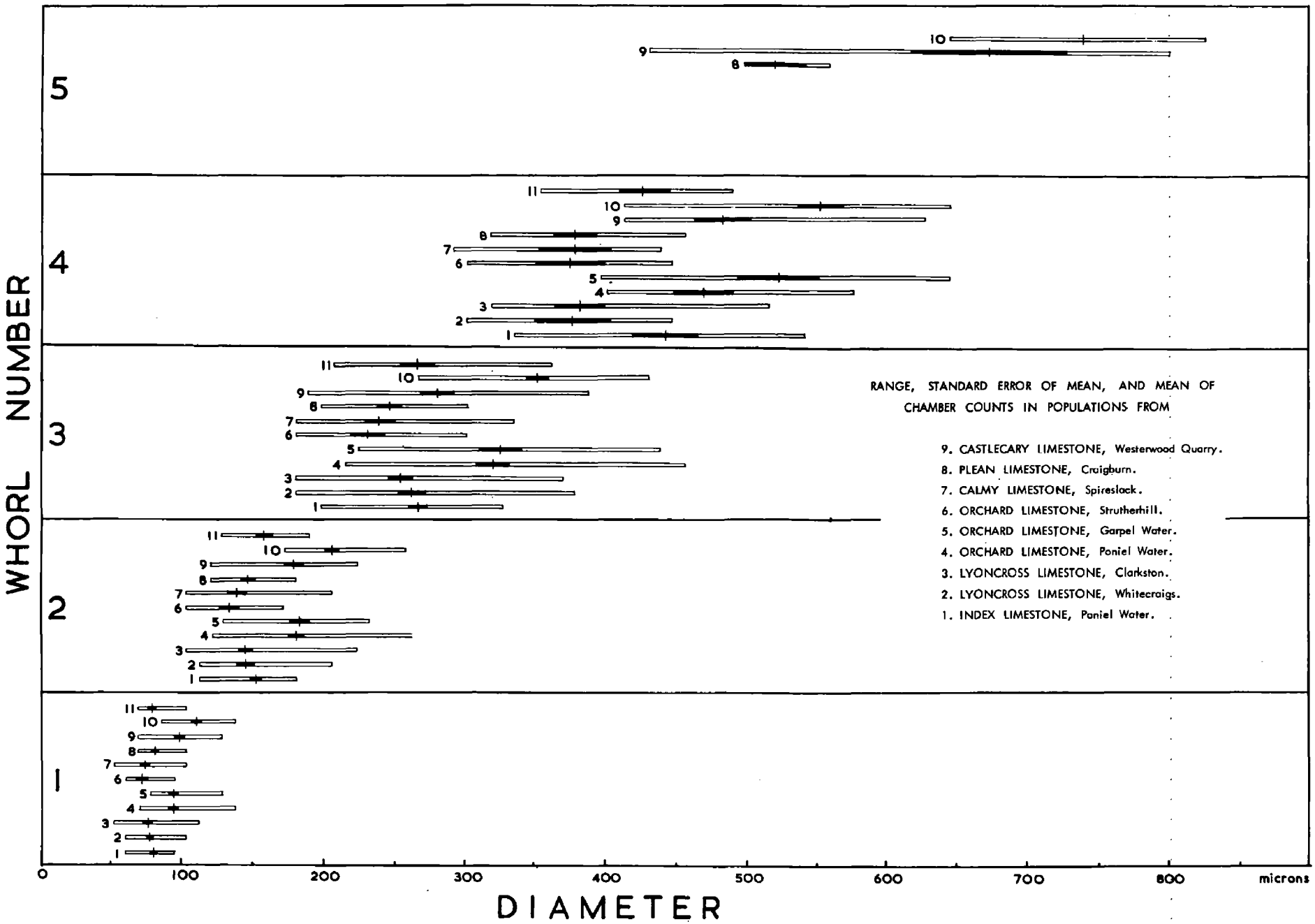
The information regarding chamber count and diameter is combined in Text fig.23, in which distinct curves are illustrated for successive limestone horizons. The more conservative group of paramillerellids in the Upper Limestone Group (Text fig.19, Nos.1-6, 13-16, 28-31, & 34-36) is represented by the four lower curves, and the more progressive and divergent group in the upper two curves. In two instances populations from the same stratigraphic level show quite different characters (see Text fig.24). It can be seen that

TEXT - FIGURE 22.

PARAMILLERELLA.

The range, standard error of the mean, and mean of diameter at successive whorls in various species of Paramillerella from a number of horizons and localities in the Upper Limestone Group.

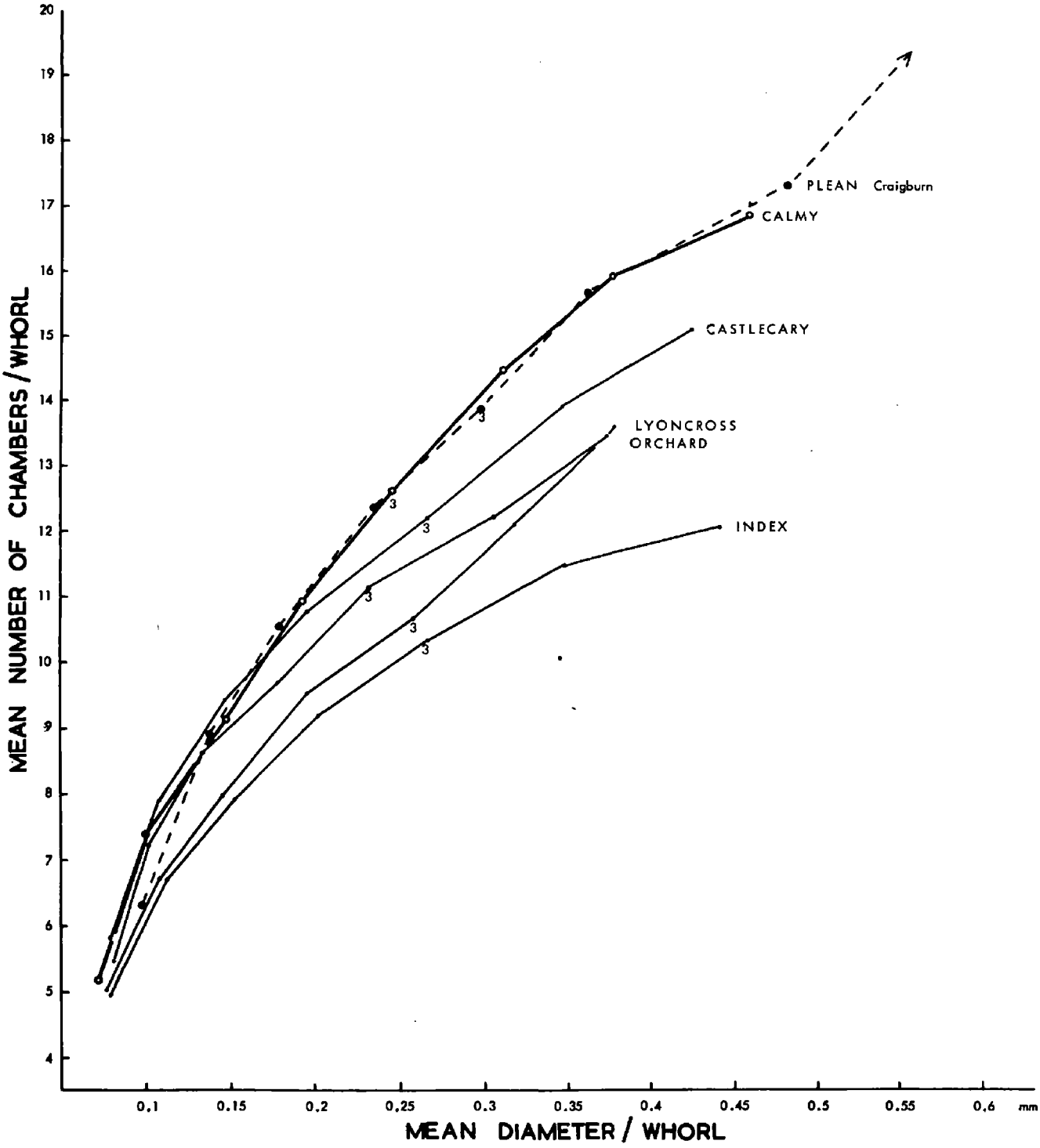
1. Index Limestone. (Paramillerella indicis indicis).
2,3. Lyoncross Limestone. (P.i. subradiata).
4,5. Lyoncross Limestone. (P. ayrensis).
6,7. Orchard Limestone. (P. radiata).
8. Calmy Limestone. (P, involuta).
9. Plean Limestone. (P. craigburnensis).
10. Plean Limestone. (P. hemisphaerica).
11. Castlecary Limestone. (P. westerwoodensis)


WHORL NUMBER
5
4
3
2
1
RANGE, STANDARD ERROR OF MEAN, AND MEAN OF CHAMBER COUNTS IN POPULATIONS FROM
9. CASTLECARY LIMESTONE, Westerwood Quarry.
8. PLEAN LIMESTONE, Craigburn.
7. CALMY LIMESTONE, Spireslack.
6. ORCHARD LIMESTONE, Strutherhill.
5. ORCHARD LIMESTONE, Garpel Water.
4. ORCHARD LIMESTONE, Poniel Water.
3. LYONCROSS LIMESTONE, Clarkston.
2. LYONCROSS LIMESTONE, Whitecraigs.
1. INDEX LIMESTONE, Poniel Water.
0
100
200
300
400
500
600
700
800
microns
DIAMETER

TEXT - FIGURE 23.

PARAMILLERELLA.

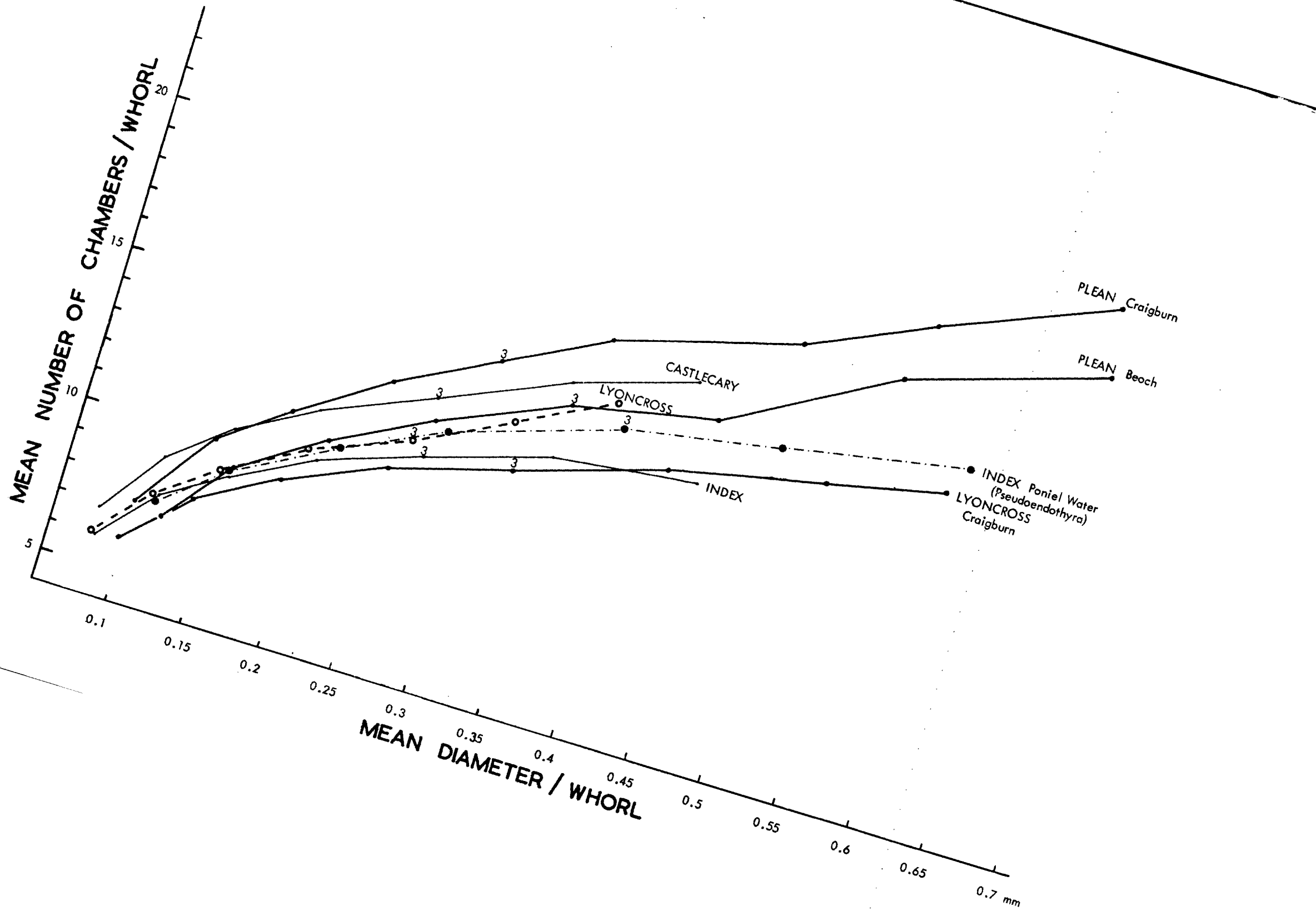
The average number of chambers per whorl plotted against the average diameter at each half whorl, starting at the first whorl and with the third whorl designated by the figure 3. The lower four curves represent the more conservative group of paramillerellids (see Text fig.19), while the upper curves represent the more divergent species.


MEAN NUMBER OF CHAMBERS / WHORL
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
PLEAN Craigburn
CALMY
CASTLECARY
LYONCROSS ORCHARD
INDEX
3
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
mm
MEAN DIAMETER / WHORL

TEXT - FIGURE 24.

PARAMILLERELLA.

The average number of chambers per whorl plotted against the average diameter at each half whorl, starting at the first whorl and with the third whorl designated by figure 3. A comparison of different populations from the Plean and Lyoncross Limestones against the background of the curves of populations from the Index and Castlecary Limestones. The curve for Pseudoendothyra diaphana sp. nov. is also compared showing that it differs in character from any of the species of Paramillerella.


MEAN NUMBER OF CHAMBERS / WHORL
5
10
15
20
MEAN DIAMETER / WHORL
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
0.7 mm
3
CASTLECARY
LYONCROSS
INDEX
PLEAN Craigburn
PLEAN Beoch
INDEX Poniel Water (Pseudoendothyra)
LYONCROSS Craigburn

the two Plean and Lyoncross populations show quite distinct and unrelated curves and it is, therefore, inferred that if these two separate populations were, indeed, contemporaneous, then it implies geographic or ecological isolation of the populations at their respect-:ive localities.

The results obtained for chamber counts and diameter are repeated essentially in form ratio, but in a less distinctive manner. (See Text figs.25,26).

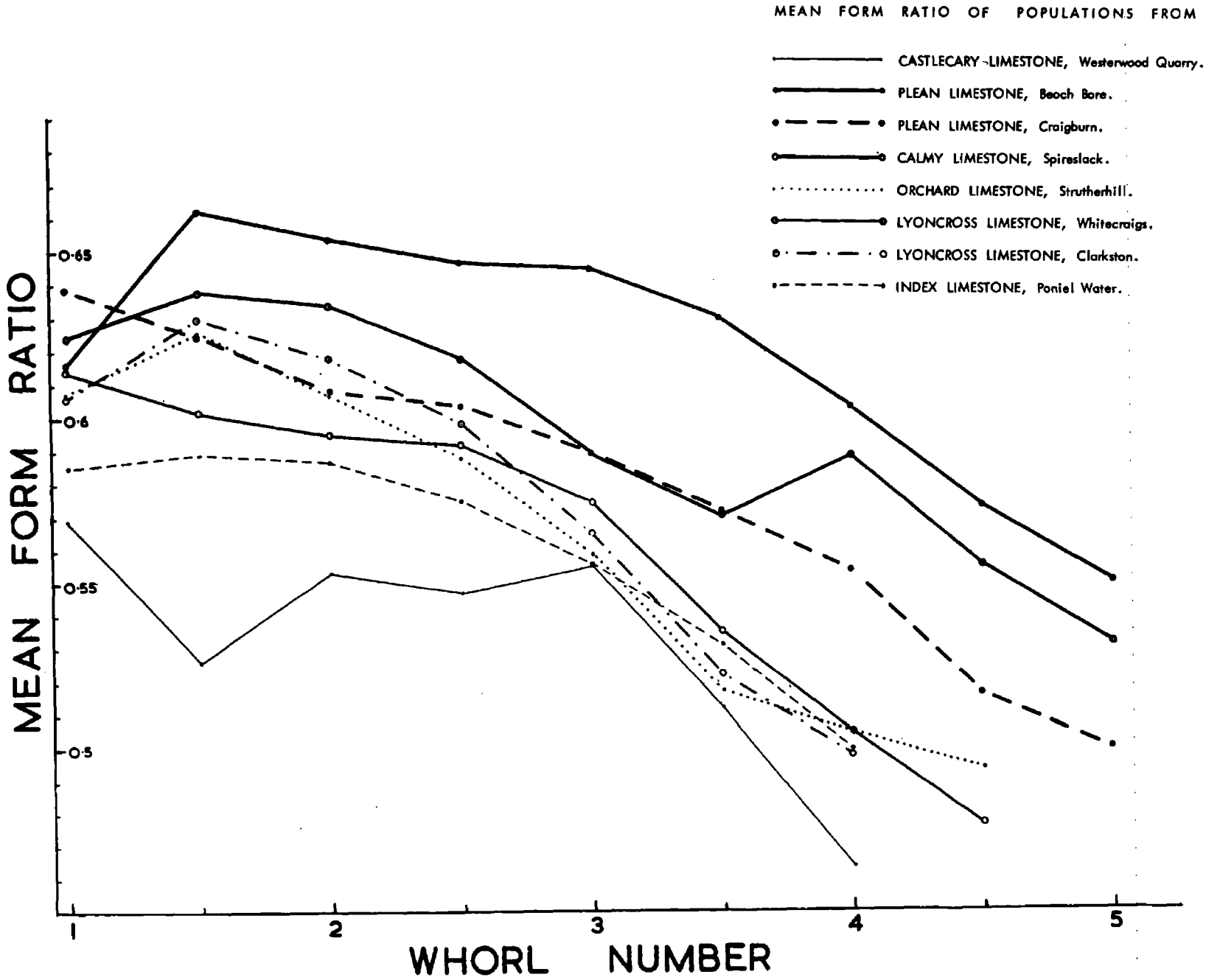
2. ENDOTHYRA.

Because of the plectogyral coiling of Endothyra it is not possible to relate the number of chambers to the whorl number and comparison of growth stages is possible only in terms of diameter. It is clear from fig. 27, that in specimens greater than 0.28 mm. the curves of diameter plotted against the number of chambers are distinct at each horizon with the variation at different localities being appreciably less than that at different horizons. It, therefore, follows that within limits the limestones may be recognised on the basis of the chamber counts in adult populations of Endothyra (Text fig.27, lower diagram). The majority of individuals have a diameter between 0.41-0.46 mm. (Text fig.28), and chamber frequency at this diameter range is compared together with that for the complete adult populations

TEXT - FIGURE 25.

PARAMILLERELLA.

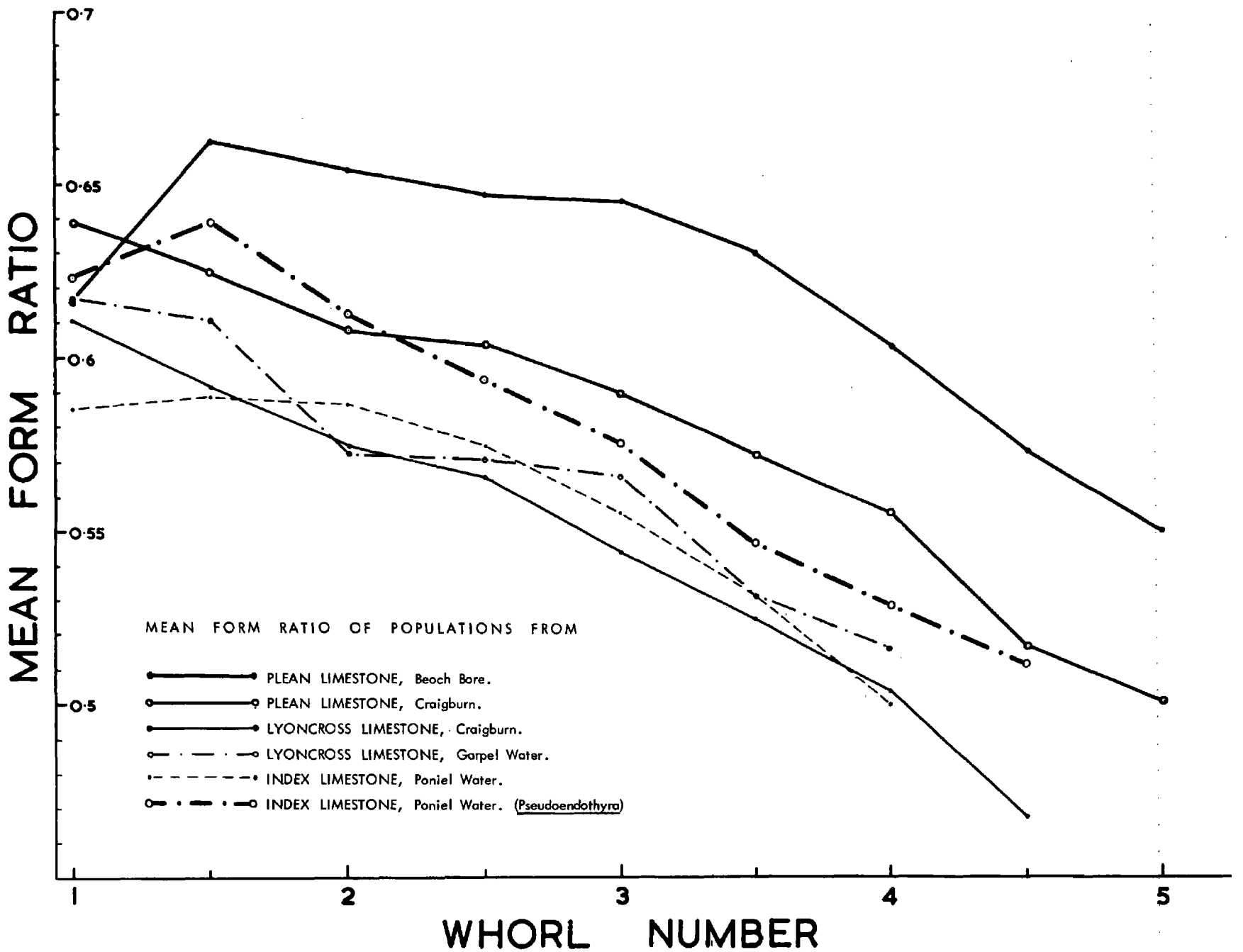
Curves of mean form ratio (axial length/ diameter) plotted against whorl number for various species from a range of horizons and localities in the Upper Limestone Group. Although some of the curves are quite distinctive there is a range in which there is considerable overlap suggesting that form ratio does not provide a particularly reliable means of discriminating the various populations.


MEAN FORM RATIO OF POPULATIONS FROM
CASTLECARY LIMESTONE, Westerwood Quarry.
PLEAN LIMESTONE, Beoch Bore.
PLEAN LIMESTONE, Craigburn.
CALMY LIMESTONE, Spireslack.
ORCHARD LIMESTONE, Strutherhill.
LYONCROSS LIMESTONE, Whitecraigs.
LYONCROSS LIMESTONE, Clarkston.
INDEX LIMESTONE, Poniel Water.
MEAN FORM RATIO
0·65
0·6
0·55
0·5
1
2
3
4
5
WHORL NUMBER

TEXT - FIGURE 26.

PARAMILLERELLA.

Curves of mean form ratio plotted against whorl number for populations from a number of horizons and localities compared with the curve for *Pseudoendothyra diaphana*.


MEAN FORM RATIO
0·7
0·65
0·6
0·55
0·5
1
2
3
4
5
WHORL NUMBER
MEAN FORM RATIO OF POPULATIONS FROM
PLEAN LIMESTONE, Beoch Bore.
PLEAN LIMESTONE, Craigburn.
LYONCROSS LIMESTONE, Craigburn.
LYONCROSS LIMESTONE, Garpel Water.
INDEX LIMESTONE, Poniel Water.
INDEX LIMESTONE, Poniel Water. (Pseudoendothyra)

(over 0.32 mm.), and it can be seen that the mode of chamber frequency shows a marked 'shift' at successive horizons. (Text fig.28).

In order to assess the validity of the differences in chamber frequency in populations of Endothyra, recourse is made to the simple test of statistical significance, the χ^2 test. When dealing with a 2 x n contingency table, there is a convenient short method of calculation χ^2 when the results are tabulated as shown in Table 47, and

$$\chi^2 = \frac{g - nG}{G(1 - G)}$$

TABLE NO.47.

Collections	Morphotypes				Totals
	1	2	3	4	
X	a	b	c	d	n
Y	A	B	C	D	N
Totals	a+A	b+B	c+C	d+D	n+N
g	$\frac{a}{a+A}$	$\frac{b}{b+B}$	$\frac{c}{c+C}$	$\frac{d}{d+D}$	g
G					$\frac{n}{n+N}$

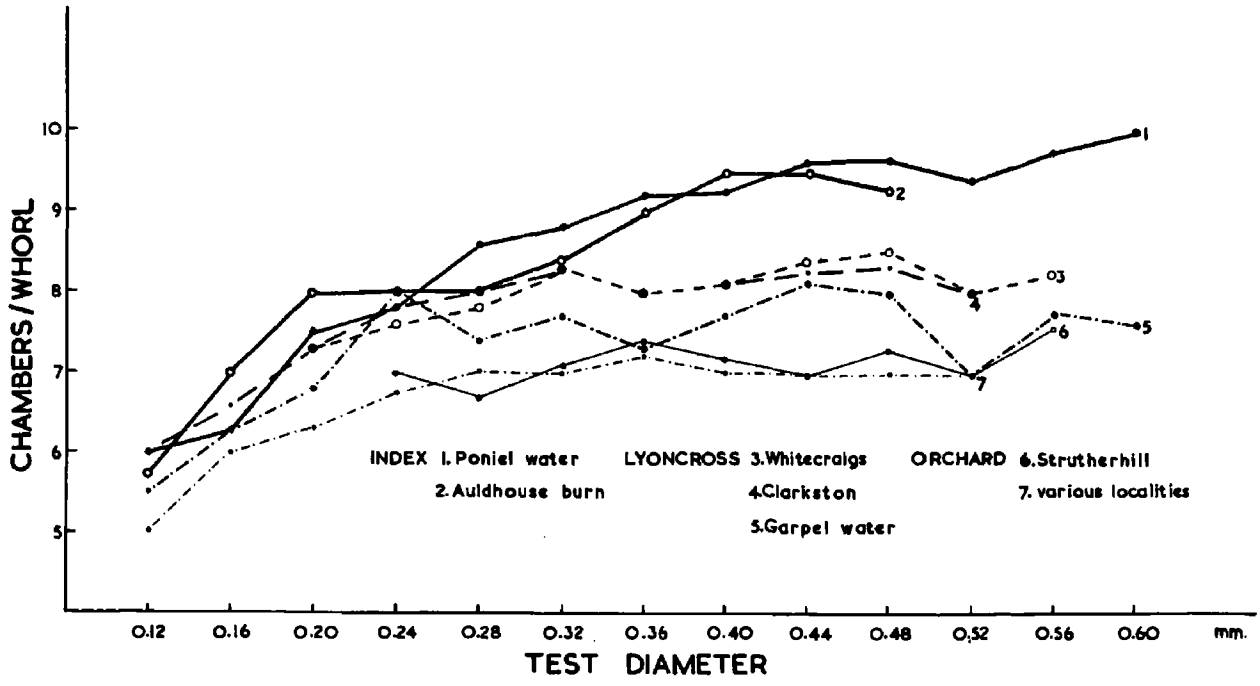
The numerical values upon which Text fig.28 is based are given below in Table 48.

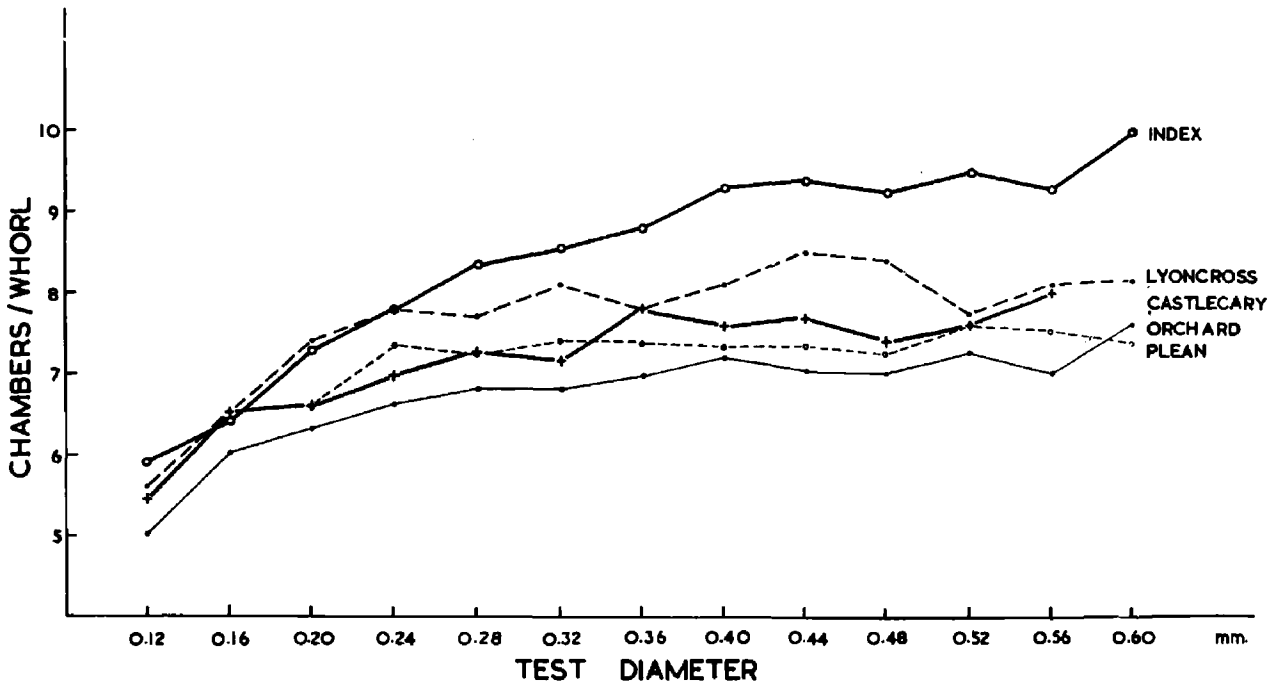
TEXT - FIGURE 27.

ENDOTHYRA.

Upper Diagram - curves showing the average number of chambers per whorl plotted against diameter in populations of Endothyra at a number of localities.

Lower Diagram - the same relationship shown as an average of all localities at each horizon. Note that each curve is distinct particularly over the size range 0.32-0.48mm. in which the majority of specimens fall.


CHAMBERS / WHORL
10
9
8
7
6
5
INDEX 1. Poniel water
2. Auldhouse burn
LYONCROSS 3. Whitecraigs
4. Clarkston
5. Garpel water
ORCHARD 6. Strutherhill
7. various localities
0.12
0.16
0.20
0.24
0.28
0.32
0.36
0.40
0.44
0.48
0.52
0.56
0.60
mm.
TEST DIAMETER


CHAMBERS / WHORL
10
9
8
7
6
5
INDEX
LYONCROSS
CASTLECARY
ORCHARD
PLEAN
0.12
0.16
0.20
0.24
0.28
0.32
0.36
0.40
0.44
0.48
0.52
0.56
0.60
mm.
TEST DIAMETER

TEXT - FIGURE 28.

ENDOTHYRA.

The left hand column shows the chamber frequencies in adult whorls of Endothyra at successive horizons. This is an average based on material from a number of localities. The centre column shows that at the majority of horizons and localities mature specimens have a diameter from 0.41-0.48mm. and, in the right hand column, the chamber frequency at this diameter class is compared at successive horizons and various localities. Note the pronounced modal shifts at each horizon.

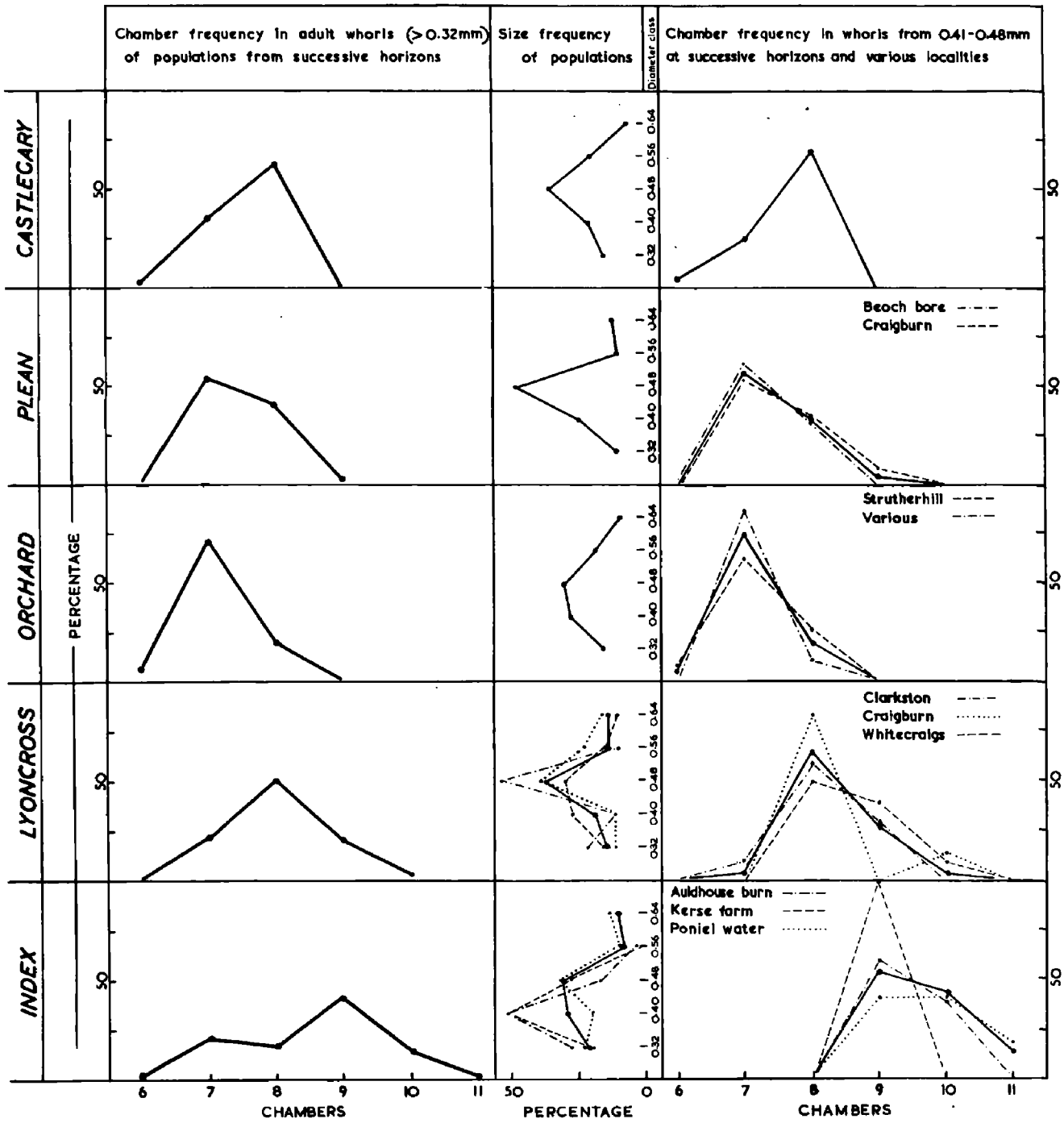

Chamber frequency in adult whorls (>0.32mm) of populations from successive horizons
Size frequency of populations
Diameter class
Chamber frequency in whorls from 0.41-0.48mm at successive horizons and various localities
CASTLECARY
PLEAN
ORCHARD
LYONCROSS
INDEX
PERCENTAGE
50
0.32 0.40 0.48 0.56 0.64
Beoch bore
Craigburn
Strutherhill
Various
Clarkston
Craigburn
Whitecraigs
Auldhouse burn
Kerse farm
Poniel water
6 7 8 9 10 11
CHAMBERS
50 0
PERCENTAGE
6 7 8 9 10 11
CHAMBERS

TABLE NO.48.

Limestone Horizon	Number of Chambers 6	7	8	9	10	11	Total
Castlecary	1	16	28	-	-	-	45
Plean	-	30	23	2	-	-	55
Orchard	4	41	12	-	-	-	57
Lyoncross	1	17	38	16	3	-	75
Index	2	22	18	42	15	2	101
Totals	8	126	119	60	18	2	333

It can be seen that in comparing the frequencies observed at the Castlecary and Plean Limestone horizons in Table 48, the expected frequencies for cells 6 and 9 fall below 5, and it is necessary to combine the information as follows:-

Horizon	Chambers 7	8	Total
Castlecary	17	28	45
Plean	30	25	55
Total	47	53	100

$$\chi^2 = \frac{20.85 - 20.25}{0.45 \times 0.55}$$

$$= 2.424$$

Thus with one degree of freedom P lies between 0.25 and 0.10. The difference is not significant and on the basis of the information available it is not possible to establish that the samples were drawn from different

populations.

Again in comparing Plean with Orchard Limestone some of the cells in Table 48 fall below 5, and it is necessary to combine the columns as follows:-

Horizon	Chambers 7	8	Total
Plean	30	25	55
Orchard	45	12	57
Total	75	37	112

$$\chi^2 = \frac{28.89 - 27.02}{0.49 \times 0.51}$$

$$= 7.4$$

Thus with one degree of freedom P lies between 0.01 and 0.005, and the result is significant.

In making the comparison of the Orchard and Lyoncross Limestone horizons it is necessary to reconstruct Table 48, as follows:-

Horizon	Chambers 7	8	9	Total
Orchard	45	12	-	57
Lyoncross	18	38	19	75
Total	63	50	19	132

$$\chi^2 = \frac{35.02 - 24.61}{0.2453}$$

$$= 41.47$$

Therefore, with 2 degress of freedom P. is much less than 0.005 and is therefore highly significant.

Finally the Lyoncross and Index Limestone horizons are compared according to the figures below:-

Horizon	Chambers 7	8	9	10	Total
Lyoncross	18	38	16	3	75
Index	24	18	42	17	101
Total	42	56	58	20	176

$$\chi^2 = \frac{38.36 - 31.97}{0.42 \times 0.57}$$

$$= 26.13$$

Thus with 3 degrees of freedom P is much less than 0.005 and again the result is highly significant.

The χ^2 test reveals that it is possible to distinguish Castlecary, Orchard, Lyoncross and Index Limestone horizons on the basis of the frequency of the chambers in adult populations of Endothyra, but it is probable that the Calmy and Plean Limestone horizons cannot be distinguished from horizons immediately above or below. This analysis, of course, treats the populations of Endothyra as morphotypes simply on the basis of the number of chambers in adult whorls. There are, however, other morphological features to be considered; the inflation of the chambers, the nature of the secondary deposits, and the degree of axial rotation. Thus, to some extent, the morphotypic analysis cuts across the accepted taxonomic grouping of species in Endothyra. The morphological

range and development of Endothyra in the Upper Limestone Group is displayed in Text fig.29, and an analysis of this morphological chart together with data regarding chamber frequency suggests that the factors controlling the development of the number of chambers in adult whorls of Endothyra are complex, and variable.

Endothyra phrissa is a relatively rare form (15% of populations) in the Index Limestone, and occurs in a similar proportion in the Lyoncross Limestone of the Central Coalfield, but in the Lyoncross Limestone of Ayrshire Endothyra phrissa has a slightly more frequent occurrence showing that ecological conditions control the population structure of E. phrissa and E. pandorae. Thus the exclusive occurrence of Endothyra phrissa at the Orchard position and, thus, the occurrence of populations with 7 chambers predominating in final whorls, most probably results from the ecological exclusion of E. pandorae rather than its phyletic extinction. On the other hand it is quite clear that populations of E. pandorae in the Index Limestone have more chambers in adult whorls (62% with 9) than those in Lyoncross Limestone (51% with 8) and, while this appears to be controlled by a bioseries modifying chamber form, it is conceivable that it could have been the result of environmental factors such as temperature and salinity as has been discussed by

TEXT - FIGURE 29.

ENDOTHYRA.

Chart showing the morphological range and development of Endothyra in the Upper Limestone Group.

Castlecary Limestone.

1-4 & 7-10. Endothyra barbata.

11 & 12. Endothyra sp.

5-6 & 11-15. Endothyra phrissa.

Plean Limestone.

1-7. Endothyra barbata.

Calmy Limestone.

8-11. Endothyra phrissa.

Orchard Limestone.

1-14. Endothyra phrissa.

Lyoncross Limestone.

1-4,8-9 & 11-16. Endothyra pandorae.

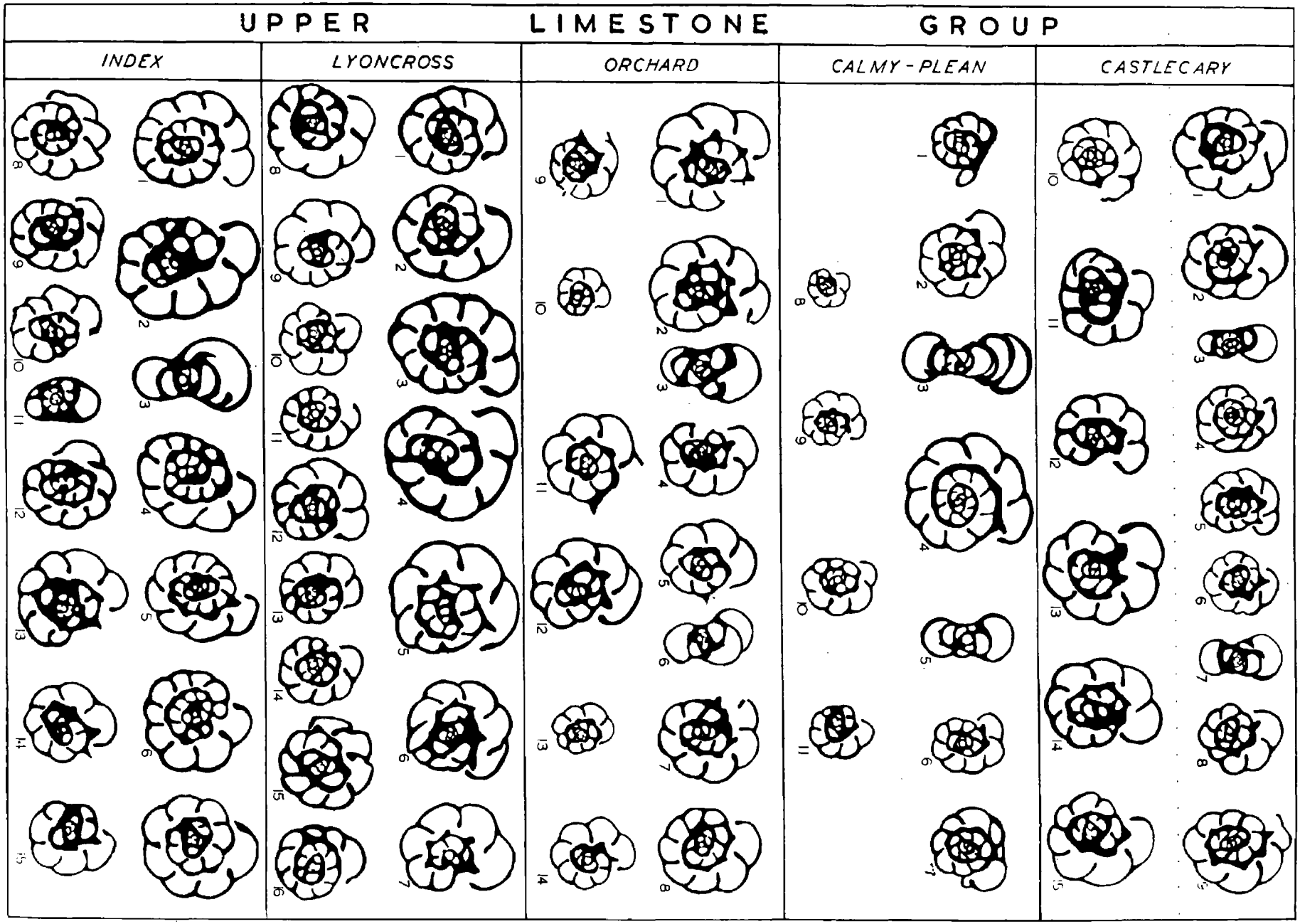
5-7 & 10. Endothyra phrissa.

Index Limestone.

1-5 & 8-12. Endothyra pandorae.

6-7. Endothyra paucinodosa.

13-15. Endothyra phrissa.


UPPER LIMESTONE GROUP
INDEX
LYONCROSS
ORCHARD
CALMY - PLEAN
CASTLECARY

Bradshaw (1957 p.1138).

At the higher horizons, Orchard to Castlecary, a distinct phylogenetic trend can be recognised involving a decrease in axial rotation, and an increasing development of basal deposits leading from E. phrissa to E. barbata, and so resulting in the change from populations 72% of which have 7 chambers in Orchard Limestone to populations in the Castlecary Limestone in which 62% have 8 chambers.

3. BRADYINA.

All the populations of Bradyina are closely similar in chamber count and dimensions, but the character of the wall varies and, thus, possibly provides a means of stratigraphical discrimination. The contrast between the walls of B. samarinaformis and B. perforata is striking and clear cut, and it is probable that these species represent stages on separate phyletic lines, and might therefore be expected to appear together. The mutually exclusive occurrence of B. samarinaformis and B. perforata, therefore, suggests that their distribution was predominantly controlled by ecological conditions.

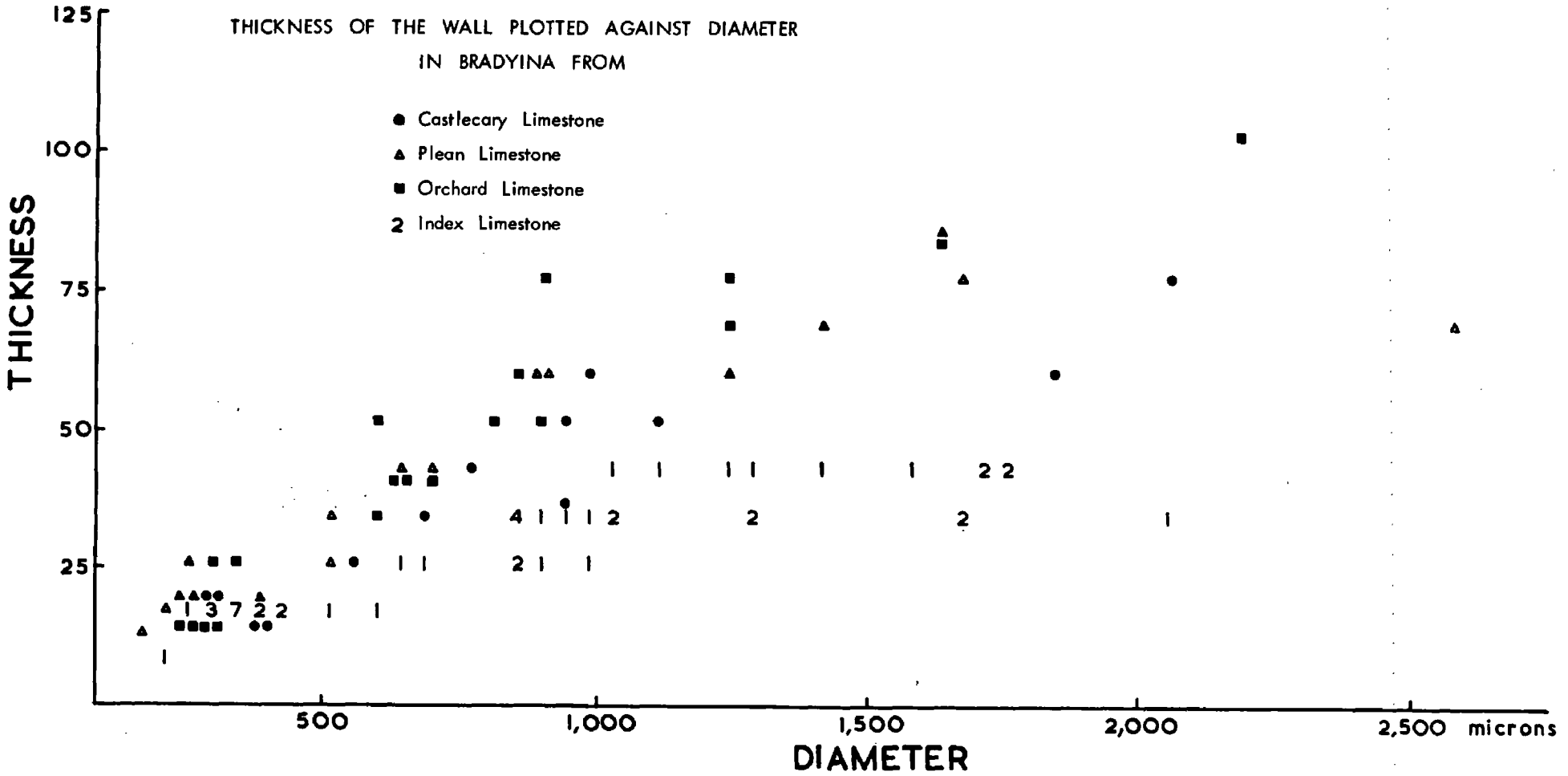
It has been noted that there is a tendency for the wall of B. perforata to become progressively thinner from the Orchard Limestone into the Plean and Castlecary

Limestones (see Table 44, p.270 and Text fig.30). Since all the limestones in which the bradyinids occur present a relatively uniform lithology it is not likely that the thickness of the wall is related to the nature of the host sediment in the manner discussed by Hendrix (1958). B. perforata may, therefore, represent an intermediate stage on a bioseries from the stout walled, coarsely alveolar, B. rotula Eichwald of the Visean to the much thinner walled B. cribrostomata of the Middle Carboniferous.

TEXT - FIGURE 30.

BRADYINA.

The thickness of the wall plotted against the diameter of the test in populations of *Bradyina samarinaformis* sp. nov. from the Index Limestone, and *B. perforata* sp. nov. from the Orchard, Plean and Castlecary Limestones. The scatter diagram suggests that there is a progressive thinning of the wall of *B. perforata* from the Orchard to the Castlecary Limestone, and shows that the wall of *B. samarinaformis* follows a quite different growth curve.


THICKNESS OF THE WALL PLOTTED AGAINST DIAMETER
IN BRADYINA FROM
Castlecary Limestone
Plean Limestone
Orchard Limestone
2 Index Limestone
THICKNESS
125
100
75
50
25
500
1,000
1,500
2,000
2,500 microns
DIAMETER

THE ASSEMBLAGES.

Within the Upper Limestone Group the assemblages often display a very distinctive character which may be quite reliably diagnostic of a particular limestone horizon although its application is restricted to the local sedimentary basin and a restricted lithological range of limestones. The character and distribution of the foraminifers within the limestones of the Upper Limestone Group is summarised below.

Index Limestone.

The following species have been identified from the Index Limestone, (see Text fig.31):-

Aoujgalia sp., Archaediscus krestovnikovi Rauser-Chernoussova, Bradyina samarinaformis sp. nov., Calcitornella? sp., Calcitrbnella cf. heathi Cushman & Waters, Calcitrbnella sp., Calcivertella? sp., Climacammina bradyi (Moeller), C. prisca Lipina, Earlandia pulchra Cummings, Endostaffella modica sp. nov., Endothyra pandorae D.N. Zeller, E. paucinodosa sp. nov., E. phrissa D.N. Zeller, Globivalvulina globulus sp. nov., Glomospira ? sp., Paramillerella indicis indicis subsp. nov., Pseudoendothyra diaphana sp. nov., Stacheoides sp., Tetrataxis quadriloba sp. nov., T. tricamerata sp. nov., Tuberitina maljavkini Mikhailov.

TEXT - FIGURE 31.

Typical assemblage of foraminifers from the Index Limestone.

1,2. Bradyina samarinaformis sp. nov.

3. Tetrataxis cf. quadriloba sp. nov.

4,5. Tetrataxis spp.

6. Climacammina cf. bradyi (Moeller).

8,9. Climacammina prisca Lipina.

10,11. Aoujgalia cf. sp. nov.

All X15 approx.

12,13. Pseudoendothyra diaphana sp. nov.

14. Endothyra paucinodosa sp. nov.

15. Endothyra phrissa (D.N. Zeller).

16,17. Endothyra pandorae (D.N. Zeller).

18-23. Paramillerella indicis indicis subp. nov.

24. Archaediscus krestovnikovi Rauser-Chernoussova

25-28. Archaediscus cf. krestovnikovi.

29-34. Endostaffella modica sp.nov.

35-36. Earlandia pulchra Cummings.

37-38. Tuberitina maljavkini Mikhailov.

39-44. Globivalvulina globulus sp. nov.

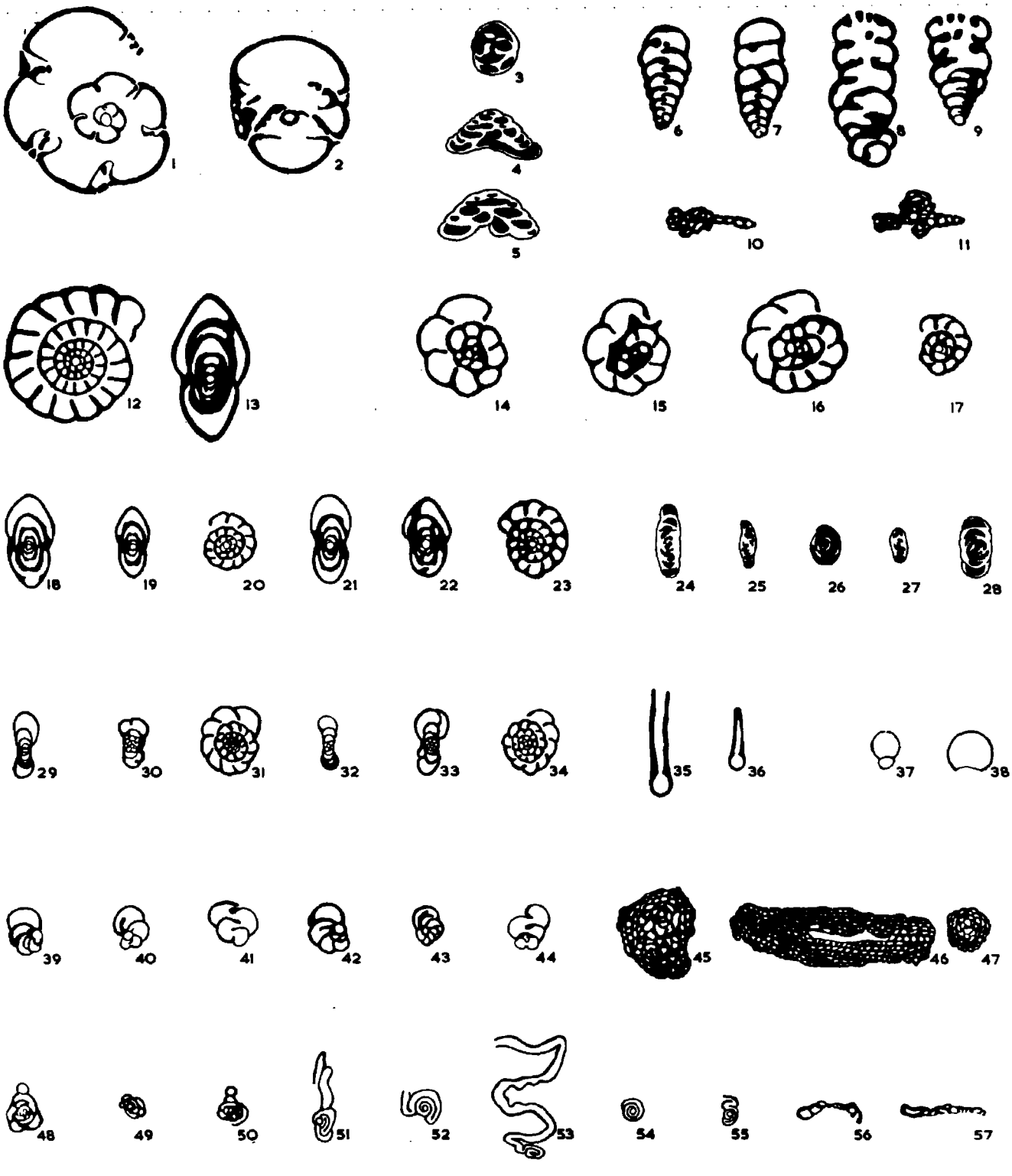
45-47. Stacheoides sp.

48-50. Glomospira? sp.

51. Calcivertella? sp.

52. Calcitrónella cf. heathi Cushman & Waters.

INDEX LIMESTONE — *FORAMINIFERAL ASSEMBLAGE*



TEXT - FIGURE 31. - cont.

53-55. *Calcitornella*? sp.

56-57. *Glomospira*? sp.

All X33 approx.

This assemblage has been recorded from only two localities, (fig. 17), and in more typical developments of the Index Limestone, the species Bradyina samarinaformis, Globivalvulina globulus, and Pseudoendothyra diaphana are absent. The most striking feature of the fauna from the Index Limestone is the great abundance of Endostaffella modica which forms a dominant part of the assemblage and, together with Endothyra pandorae, E. phrissa, E. paucinodosa and Paramillerella indicis indicis, makes up 50 to 60% of the assemblage. The palaeotextulariids occur sporadically and appear to favour the cleaner bioclastic limestones. Tetrataxis occurs abundantly only in the strongly bioclastic bands in the limestone which may form small lensoid microcoquinas less than one centimetre in thickness. Sometimes the micro-:coquinas are cemented by sparry calcite but most commonly the interstices of the debris are filled by the argillaceous lime mud. Where small sparry bioclastic pockets occur, they often contain large numbers of foraminiferal tests. The Index Limestone is fine grained as a rule, with much fine bioclastic debris. The larger fragments of the bioclastic debris often have a finely banded coating of tangled fine sinuous Girvanella. In some cases the algal coatings are completely recrystallised and replaced and

impregnated by pyrite to form Osagia like nodules. With the fine bioclastic debris are associated abundant encrusting benthonic foraminifers of the families Fischerinidae and Ptychocladiidae. The small species Archaediscus krestovnikovi occurs ubiquitously and the main control on its relative abundance appears to be the state of recrystallisation in the limestone.

An impoverished assemblage is typical of the Index Limestone in the east of the Midland Valley but, as in the west, the proportions and abundance of the species of Endostaffella, Endothyra, and Paramillerella distinguish the assemblage.

Lyoncross Limestone.

The following foraminifers have been identified in the Lyoncross Limestone (Text fig.32): Aoujgalia sp. nov. Archaediscus krestovnikovi, Gen. et. sp. nov. Cummings (1961 p.117), Archaediscus cf. grandiculus. Schlykova, Bradyina cf. perforata sp. nov., Calcitornella cf. heathi, Calcivertella cf. adhaerens Cushman & Waters, Calcivertella sp., Paramillerella (Chernousovella) sp., Climacammina antiqua (Brady), Earlandia pulchra, E. cf. vulgaris (Rauser - Chernoussova & Reitlinger), Endostaffella modica, Endothyra pandorae, E. phrissa, Globivalvulina globulus, Glomospira ? sp. Glomospira ? ishimbaica Lipina, Helicospirina plicata

TEXT - FIGURE 32.

The assemblage of foraminifers recorded from the Lyoncross Limestone.

1-10. Climacammina antiqua (Brady)

11. Climacammina cf. bradyi (Moeller).

12. Climacammina antiqua (Brady).

13-14. Aoujgalia sp. nov.

15-19. Tetrataxis tricamerata sp. nov.

20-28. Paramillerella ayrensis sp. nov.

29-34. Paramillerella indicis subradiata subsp.nov.

35-36. Archaediscus cf. krestovnikovi Rauser-Chernoussova.

37. Archaediscus cf. grandiculus Schlykova.

38. Archaediscus krestovnikovi Rauser-Chernoussova.

39. Gen et sp. nov. Cummings (1961 p.117).

40. Archaediscus sp.

41,44. Endothyra phrissa (D.N. Zeller).

42-43 & 45,46. Endothyra pandorae (D.N. Zeller).

47-49. Globivalvulina globulus sp. nov.

50-57. Endostaffella modica. sp.nov.

58-59. Glomospira? cf. ishimbaica Lipina.

60. Glomospira sp.

61-67. Helicspirina plicata (Brady).

70-71. Earlandia pulchra Cummings.

72-74, 76 & 78. Calcivertella cf. adhaerens Cushman & Waters.

LYONCROSS LIMESTONE — *FORAMINIFERAL ASSEMBLAGE*

TEXT - FIGURE 32. - cont.

75. Calcivertella? sp.

77. Calcitornella heathi Cushman & Waters.

79-80. Stacheoides sp.

All X30 approx.

sp. nov., Paramillerella ayrensis sp. nov., P. indicis subradiata subsp. nov., Stacheoides sp. Tetrataxis tricamerata sp. nov. Tuberitina maljavkini.

Two distinct assemblages have been recognised at this horizon. In the Central Coalfield area the assemblage is closely similar to that in the Index Limestone, and is characterised by the abundance of the species Endostaffella modica together with slightly less abundant Paramillerella indicis subradiata, Endothyra phrissa, and E. pandorae. In the Lyoncross Limestone of Ayrshire and South Lanarkshire, the proportions of the assemblage are totally different (Text fig.18) and Endostaffella modica, together with the species of Endothyra, is greatly reduced in numbers. Paramillerella ayrensis replaces P. indicis subradiata while Climacammina antiqua and Globivalvulina globulus form an important part of the assemblage along with very numerous encrusting genera of the Fischerinidae. One of the most striking features of the assemblage in Ayrshire and South Lanarkshire is the large size of many of the species which may reflect unfavourable conditions of temperature and salinity (Bradshaw, 1957). The only obvious contrast in the lithology of the two areas is in the more silty, argillaceous character of the limestone in Ayrshire and South Lanarkshire and the absence of encrusting Girvanella on the bioclasts.

Orchard Limestone

The following species have been identified in the Orchard Limestone, and the typical assemblage is illustrated in text fig.33:

Agathammina ? robertsoni (Brady), Aoujgalia sp. Archaediscus krestovnikovi, A. cf. grandiculus, Gen. et sp. nov. Cummings, (1961 p.117), Bradyina perforata sp.nov., Calcitornella cf. heathi, Calcivertella cf. adhaerens, Calcivertella sp., Chernousovella sp. Climacammina antiqua (Brady), C. supraparva Cummings, C. cf. bradyi, Earlandia vulgaris, Endostaffella inflata, Endothyra phrissa, Globivalvulina globulus, Glomospira ? sp. Lugtonia elongata Cummings, L. minima Cummings, Novella minuta sp. nov., Paramillerella radiata (Brady), Stacheoides polytrematoides (Brady), Tetrataxis tricamerata, Tuberitina maljavkini.

The Orchard Limestone, although frequently strongly bioclastic and crinoidal, is typically highly argillaceous. Its fauna remains constant as does the lithology throughout the Midland Valley, and the characteristic assemblage has been recognised in the Midlothian Coal-:field area as well as in the west. The assemblage is distinguished by abundant paramillerellids with thick secondary depostis and heavy chomata. The very large species Earlandia vulgaris is very abundant and

TEXT - FIGURE 33.

The assemblage of foraminifers recorded from the Orchard Limestone.

1-4. Bradyina perforata sp. nov.

5,8. Climacammina prisca Lipina.

6,7. Climacammina bradyi (Moeller).

9,13. Earlandia vulgaris (Rauser-Chernoussova & Reitlinger).

14.15. Aoujgalia sp.

16,17. Climacammina spp.

18. Climacammina antiqua (Brady).

19,21. Tetrataxis tricamerata sp. nov.

All X15 approx.

22-27. Paramillerella radiata (Brady).

28-30. Endothyra phrissa (D.N. Zeller).

31-35. Endostaffella inflata sp. nov.

36-38. Novella minuta sp. nov.

39-44. Archaediscus cf. grandiculus Schlykova.

45-47. Gen et sp. nov. Cummings (1961 p.117).

48-49. Glomospira? cf. ishimbaica Lipina.

50. Glomospira? sp.

51,52. Calcivertella? sp.

53,54. Calcitornella? sp.

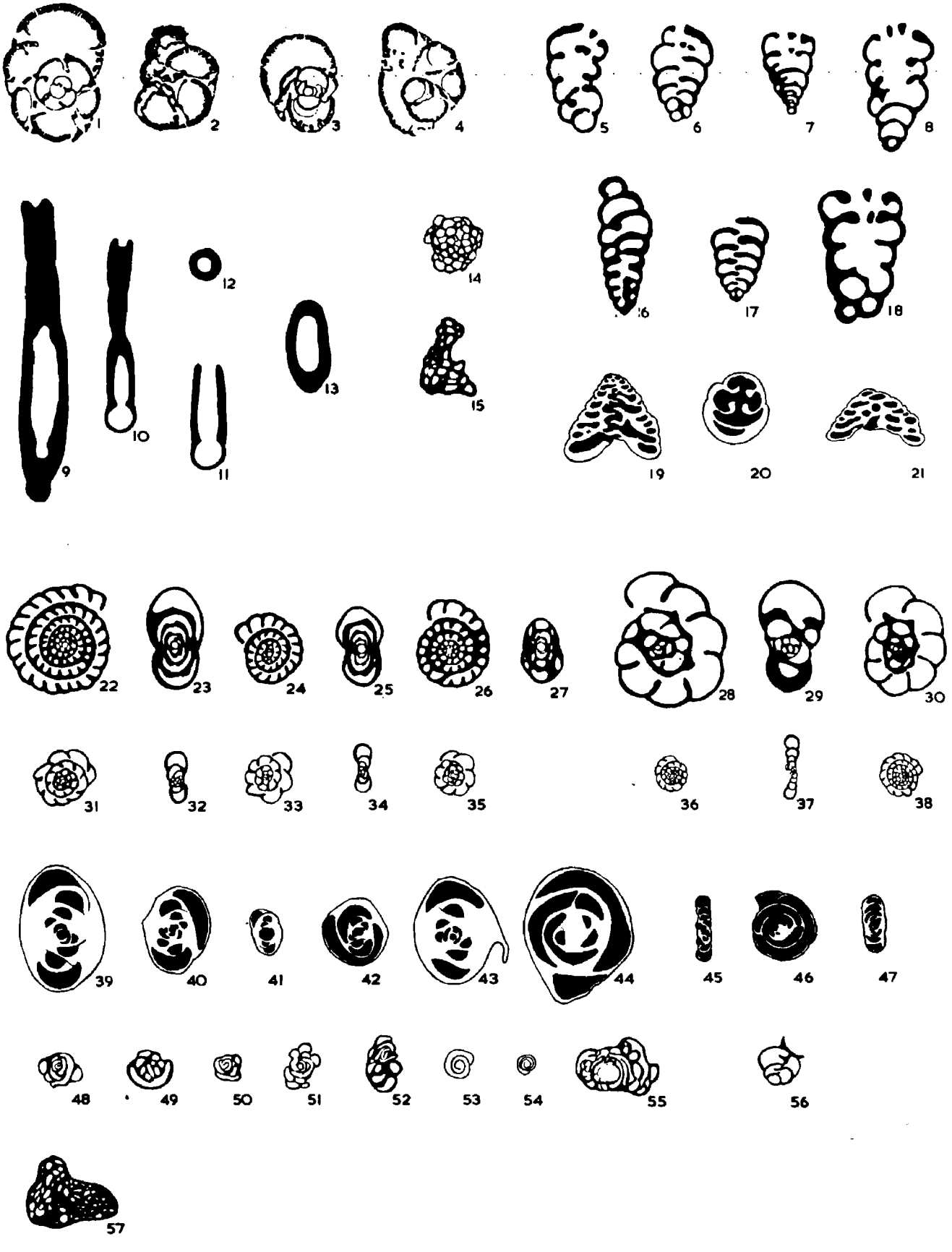
55. several individuals of Calcivertella sp.

56. Globivalvulina globulus sp. nov.

57. Stacheoides sp.

All X30 approx.

ORCHARD LIMESTONE — *FORAMINIFERAL ASSEMBLAGE*



appears to be restricted to the Orchard position alone within the Upper Limestone Group. Archaediscus cf. grandiculus is a very characteristic form in the Orchard Limestone with an abundant and widespread occurrence, and, while it has also been recorded from the Lyoncross and Castlecary Limestones it is an extremely rare form at these positions. Among other species which, while not having a restricted range, form a very typical element of the Orchard fauna, are Endostaffella inflata, Endothyra phrissa and Novella minuta. The fauna of benthonic foraminifers is much poorer than that in other limestones although there is no lack of bioclastic debris. Stacheoides polytrematoides, however, occurs quite commonly as an encrustation on crinoid columnals. The first appearance of Agathammina?robertsoni in the Upper Limestone Group is at this position. It is a relatively rare form, reaching its maximum abundance in the calcareous shale facies but never attaining the frequency of Gen. et sp. nov. Cummings (1961 p.117), or the slightly less common Archaediscus krestovnikovi. The species of Lugtonia are restricted entirely to the calcareous shale facies, and have not been observed in the limestones.

Calmy Limestone.

The following species have been identified from

the Calmy Limestone (Text fig.34):

Agathammina?robertsoni, Archaediscus krestovnikovi, Gen. et sp. nov. Cummings (1961 p.117), Bradyina perforata, Cepekia centrifuga (Brady), Cornuspira Climacammina cf. bradyi, C. supranarva, Earlandia pulchra, Endostaffella inflata, Endothyra phrissa, Globivalvulina globulus, Helicospirina sp. Novella minuta, Paramillerella radiata, P. involuta, Tetrataxis sp. Tuberitina maljavkini.

Although the Calmy is the thickest limestone in the Upper Limestone Group, it has the poorest foraminif-:eral fauna. Indeed, it may be said that the Calmy Limestone is distinguished by its lack of foraminifers. In typical developments the limestone consists of argillaceous micrites with scattered fine grained bioclastic debris. This lithology remains constant throughout most of the Midland Valley, but becomes increasingly argillaceous towards the east, and sandy in the Midlothian Coalfield area. In addition to being scarce, the foraminifers are consistently of small size and it is not clear whether this results from grain sorting or through dwarfing from unfavourable conditions of environment. The small archaediscid species such as Agathammina ? robertsoni, Archaediscus krestovnikovi and Gen. et sp. nov. Cummings (1961 p.117), are relatively common, and are associated with common, but

TEXT - FIGURE 34.

The assemblage of foraminifers recorded from the Calmy Limestone.

1. Bradyina sp.
2. Tetrataxis sp.
3. Climacammina cf. supraparva Cummings.
4,5. Climacammina sp.

All X15 approx.

6-8. Paramillerella involuta sp. nov.
9,10. Endothyra phrissa (D.N. Zeller).
11,12. Endostaffella sp.
13-15. Novella minuta sp. nov.
16. Globivalvulina globulus sp. nov.
17. Helicospirina sp.
18-21. Gen et sp. nov. Cummings (1961 p.117).
22-24. Glomospira? sp.
25. Cornuspira intermedia Waters.
26-30. Cepekia centrifuga (Brady).

All X30 approx.

CALMY LIMESTONE — *FORAMINIFERAL ASSEMBLAGE*

less abundant, Endostaffella inflata and small individuals of Endothyra phrissa. The larger species have a very sporadic occurrence and are commonly found only in the rare more coarse grained pockets of bioclasts in the limestone which suggests that size range of the foraminifers may be controlled by winnowing during sedimentation.

So far as can be determined the Calmy fauna does not differ materially from that observed in the Orchard Limestone, although Earlandia vulgaris and Archaediscus cf. grandiculus, which are so characteristic of the Orchard position, have not been recorded.

In the calcareous bioclastic shales and associated thin argillaceous bioclastic limestones overlying the Calmy Limestone a very characteristic facies fauna is developed which has been found only at this position in the Upper Limestone Group. The species which is most characteristic is Cepekia centrifuga, which often occurs in great numbers in the thin limestones. It is associated with abundant individuals of the species Novella minuta and Gen. et sp. nov. Cummings (1961 p.117). Paramillerella involuta and Endothyra phrissa also occur, but not so abundantly. A striking feature is the complete lack of the normally abundant Fischerinidae, which appear to have a mutually exclusive distribution with Cepekia centrifuga, suggesting that

this is a specialised fauna associated only with a narrow range of facies.

Plean Limestone:

At Craigburn it has been found that, in association with the rich development of corals, the foraminifers are extremely scarce. From the examination of a large number of rock slices amounting to an area of several square feet, cut for the study of the coral, it has been possible to establish the following assemblage:-

Agathammina? robertsoni, Archaediscus krestovnikovi, Bradyina perforata, Calcivertella sp. Calcitrionella sp. Climacammina supraparva, Earlandia pulchra, Endothyra barbata sp. nov., Paramillerella craigburnensis, Tetrataxis tricamerata, Tuberitina maljavkini.

Three of the species, Bradyina perforata, Climacammina supraparva, and Tetrataxis tricamerata, are known only from a single individual from which, fortunately, it has been possible to obtain a section revealing diagnostic biocharacters. At Craigburn the foraminifers usually have a sporadic occurrence with a frequency in thin sections of not more than 0.3 fragments per square centimetre. The most common species are Earlandia pulchra and Endothyra barbata with many of the irregularly enrolled and encrusting

TEXT - FIGURE 35.

The assemblage of foraminifers recorded from the Plean Limestone.

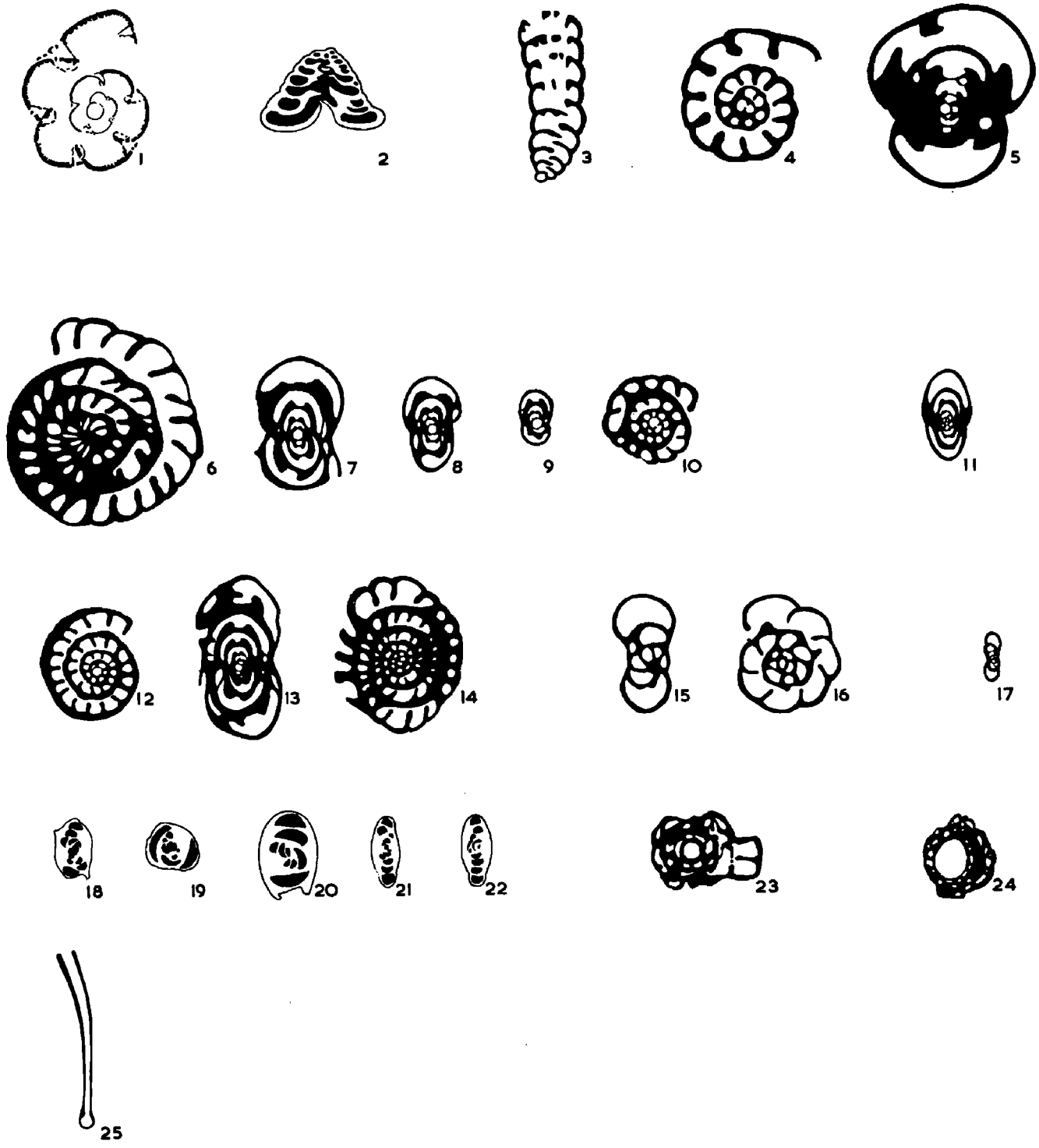
1. Bradyina perforata sp. nov.
2. Tetrataxis tricamerata, sp.nov.
3. Climacammina supraparva Cummings.
4,5. Endothyranopsis sphaerica (Rauser-Chernoussova, Beljaev & Reitlinger).

All X15.

6-10. Paramillerella hemsphaerica sp. nov.
11. Paramillerella cf. westerwoodensis sp. nov.
12-14. Paramillerella craigburnensis sp. nov.
15-16. Endothyra barbata sp. nov.
17. Endostaffella sp.
18-20. Archaediscus karreriformis Reitlinger.
21-22. Archaediscus krestovnikovi Rauser-Chernoussova.
23. Aoujgalia sp.
24. Stacheoides sp.
25. Earlandia pulchra Cummings.

All X30.

PLEAN LIMESTONE — *FORAMINIFERAL ASSEMBLAGE*



Fischerinidae, while occurring about half as frequently as these forms are Paramillerella craigburnensis, and the small archaediscids.

At Beoch there is quite a marked contrast in the fauna, the typical assemblage having the following forms:-

Archaediscus krestovnikovi, Archaediscus karreriformis Reitlinger, Bradyina perforata, Climacammina supraparva, Endostaffella modica, Endothyra barbata, E. phrissa, Endothyranopsis sphaerica, Paramillerella subsphaerica, Paramillerella cf. westerwoodensis, Tetrataxis triloba.

The most striking feature of this assemblage is the abundance of the large paramillerellid, P. subsphaerica, which forms about one third of the assemblage. Small archaediscids are plentiful, including the species A. karreriformis which appears first at this horizon, as also does Endothyranopsis sphaerica, thereby indicating the affinities of this fauna to the assemblages of the Castlecary Limestone. Endostaffella modica reappears in relative abundance, but the most abundant, if least significant, elements of the fauna are the exceedingly numerous irregularly coiled Fischerinidae. The Beoch assemblage compares very closely indeed with that seen in the Fell Top Limestone at Harlow Hill, Northumberland, where the typical coral assemblage of the Plean Limestone is also developed. The only

significant difference in the faunas is that P. hemisphaerica is absent while P. westerwoodensis is relatively abundant.

A thin limestone outcropping in a small stream between Milton and Banks has the following fauna:-

Aoujgalia, Archaediscus karreriformis, A. krestovnikovi, Calcivertella sp., Calcitornella sp., Climacammina sp., Endostaffella modica, Endothyra cf. barbata, Endothyra sp., Endothyranopsis cf. sphaerica, Helicospirina sp., Paramillerella westerwoodensis.

Although there are no corals developed at this locality, the fauna and the lithological setting suggest that, in all probability, this is the Plean No.1 Limestone. The lithology is very strongly bioclastic, but it is also argillaceous, and as a result the fauna is very badly crushed and distorted, particularly the endothyrid genera Paramillerella, Endothyra and Endostaffella. The lithology is reminiscent of the Pell Top Limestone at Newton, but lacks the corals. The Milton limestone has also a much poorer fauna without B. perforata and other large species, such as Climacammina supraparva, Tetrataxis tricamerata, and the large paramillerellids.

The most striking feature of the assemblages of the three localities discussed, is the difference in the species of Paramillerella. Nevertheless, the

associated species are sufficiently similar to suggest that the assemblages are of the same age, although at any particular locality the numbers and variety of species are clearly controlled by the kind of facies in which they occur.

Castlecary Limestone.

The fauna of the Castlecary Limestone is probably the richest of the Upper Limestone Group, and it includes: (See Text fig.36):-

Agathammina? robertsoni, Aoujgalia sp., Archaediscus cf. grandiculus, A. karreriformis, A. krestovnikovi Gen et sp. nov., Cummings, Bradyina perforata, Calcivertella sp. Climacammina antiqua, C. cf. bradyi, C. supraparva, Cornuspira intermedia (Waters) Earlandia pulchra, Endostaffella modica, Endothyra phrissa, E. barbata, Endothyranopsis sphaerica, Globivalvulina parva Chernysheva, Glomospira dubilicata Lipina, Novella minuta, Palaeonubecularia rustica Reitlinger, Paramillerella westerwoodensis, Stacheoids polytrematoides, Tetratxis tricamerata, T. triloba, Trochammina scotica, Tubertina maljavkini.

The Castlecary Limestone is very badly recrystallised throughout much of its outcrop in the eastern part of the Midland Valley. The thick upper post of the

TEXT - FIGURE 36.

The assemblage of foraminifers recorded from the Castlecary Limestone.

1,2. Bradyina perforata sp. nov.

3,4. Climacammina cf. antiqua (Brady),

5,6. Climacammina cf. bradyi (Moeller).

7,8. Climacammina supraparva Cummings.

9,13. Endothyranopsis sphaerica (Rauser-Chernoussova Beljaev & Reitlinger).

14. Tetrataxis tricamerata sp. nov.

15. Tetrataxis triloba sp. nov.

16-19. Palaeonubecularia rustica Reitlinger.

All X15 approx.

20-23. Paramillerella westerwoodensis sp. nov.

24,25. Endothyra phrissa (D.N. Zeller).

26. Endothyra barbata sp. nov.

27-29. Endostaffella modica sp. nov.

30,31. Novella minuta sp. nov.

32-37. Globivalvulina parva Chernysheva.

38-46. Trochammina scotica sp. nov.

47-50. Archaediscus karreriformis Reitlinger.

51-55. Archaediscus krestovnikovi Rauser-Chernoussova

56-62. Calcivertella spp.

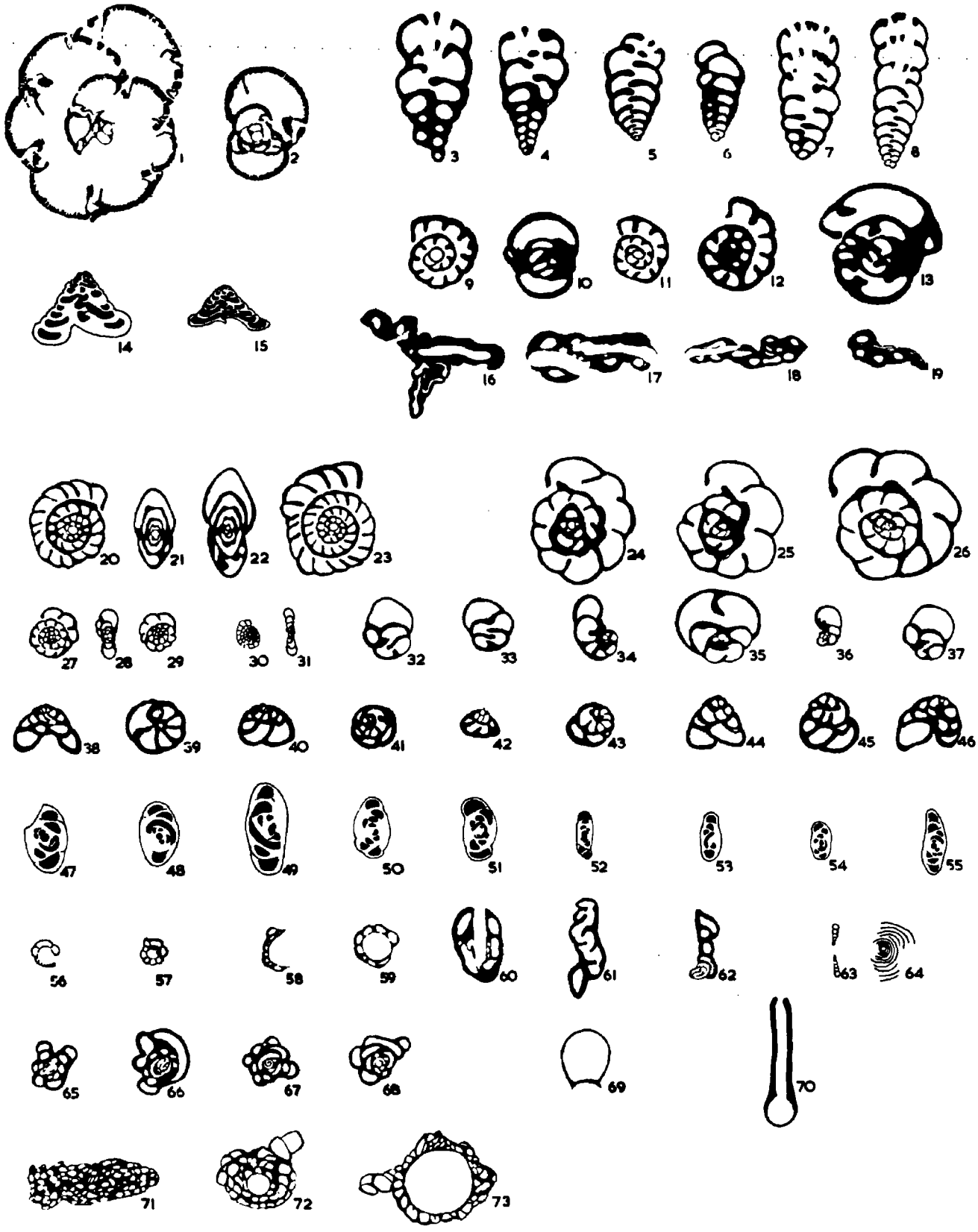
63-64. Cornuspira intermedia Waters.

65-68. Glomospira? dublicata Lipina.

69. Tuberitina maljavkini Mikhailov,

70. Earlandia pulchra Cummings.

CASTLECARY LIMESTONE — *FORAMINIFERAL ASSEMBLAGE*



TEXT - FIGURE 36. - cont.

71. Stacheoides sp.

72. Stacheoides polytrematoides (Brady).

All X30 approx.

limestone is typically a buff to yellow, coarse grained, sugary dolomite, and only under the most exceptional conditions of preservation (Plate 4, figs.1-4) does foraminiferal material survive the dolomitisation. The lower post of the limestone shows a somewhat better state of preservation but, nevertheless, material containing well preserved fauna is known only from Westerwood Quarry, near Castlecary. At Bowdenhill, near Linlithgow, the whole limestone is recrystallised but the fauna is largely recognisable, although somewhat shadowy.

The uniform character of the lithology of the Castlecary Limestone, together with the small amount of information which can be gleaned from pyritised and dolomitised relict faunas, suggest that the assemblage was constant in character throughout the limestone.

The lower post of the Castlecary Limestone has a very rich algal fauna; fine sinuous tangled Girvanella tubules coat the bioclasts to form Osagia like nodules together with scraps of entangled bioclastic debris, which are possibly picked up during the rolling of the nodule when winnowed by gentle currents. Commonly, intimately associated with the nodules are the foraminifers Palaeonubeculariа rustica, and sheet-like masses of Girvanella sp. nov. (cf. Girvanella ducii Wethered), which has a considerably greater diameter

than the tubules forming the main coating of the debris. The sheet-like masses of Girvanella occur abundantly also in the matrix, where they appear as chain like lines of contiguous tubules in transverse sections, and as curvilinear subparallel sheets in longitudinal sections. Coelosporella occurs as small convex discs, and is particularly abundant within limited bands in the limestone.

A striking feature of the encrusting benthonic foraminifers of the Castlecary Limestone is the large number of these forms which, in section, have a completely circular interior cavity, indicating that they were attached to some tubular object of which there is now not the slightest trace, the interior of the foraminifer being filled by spar or the calcareous ooze of the matrix. Empty tubular cavities have been noted so commonly that it is suggested that the sea-floor at this time must have been inhabited by a marine weed or alga, to the tubular stems or fronds of which the benthonic forms became attached. On the death or decay of the weed or alga, the small encrusting foraminifers would be left with hollow cylindrical, or strongly curved areas of attachment (Plate 29, figs.6-8).

The foraminiferal assemblage of the Castlecary Limestone is distinguished by the appearance of a number of species which occur only at this horizon, notably

Globivalvulina parva, Trochammina scotica, Glomospira? dubilicata, Palaeonubecularia rustica, Tetrataxis triloba. Other species which, although known from lower horizons, have a maximum abundance at this position are Endothyranopsis sphaerica, Archaediscus karreriformis, Bradyina perforata, Paramillerella westerwoodensis, Cornuspira intermedia.

Summary.

Contrasting the foraminiferal fauna of the Upper Limestone Group in a general way with typical upper Visean assemblages, a number of important features emerge which serve to distinguish Namurian from Visean assemblages of foraminifers.

1. Among the palaeotextulariids, Climacammina is the dominant form, and genuine species of simpler genera Cribrostomum or Palaeotextularia appear to be very rare or, indeed, entirely lacking.
2. Small archaediscid species are very abundant and show a number of distinctive morphological specialisations resulting in forms such as Agathammina? robertsoni, and Gen et sp.nov. Cummings (196. p.117). The large form Archaediscus cf. grandiculus, is also distinctive if somewhat less common than small archaediscids.

3. The paramillerellids develop rectangular chamber form and have a greater number of chambers than any of the typical Visean species.
4. The species of Endothyra show considerable variation, but are characterised by two distinctive morphological groups, both of which are in marked contrast to more strongly hooked and axially rotated forms of the upper Visean:
   a) species having a large number of chambers, moderate axial rotation, no hooks, and a moderately thick basal layer with low nodes;
   b) species having low axial rotation, prominent terminal hook and thick basal layer of secondary deposits.
5. Bradyina shows characteristic structure and thickness in its wall which suggests that two differing phyletic lines may be represented. In the more important of these a form closely allied to Janischewskina occurs, but with a distinctly thicker and slightly more coarsely alveolar wall, suggesting a transition to forms such as Bradyina concimna and Glyphostomella.
6. The abundance of species such as Novella minuta, Endostaffella modica and E. inflata may be diagnostic of Namurian strata, although species of these genera occur abundantly in the Visean.

7. The development in Tetrataxis of species with three chambers in each whorl appears to be an important characteristic of Namurian faunas.
8. The abundant occurrence of Globivalvulina is probably characteristic of Namurian faunas, particularly those of more advanced morphology such as Globivalvulina parva.
9. The predominant occurrence of Endothyranopsis sphaerica rather than E. crassa, is a useful although not entirely reliable indication of a Namurian age for the assemblages.
10. The absence of such typical upper Visean genera as Howchinia, Cribrospira, Valvulinella and Janischewskina appears to be the result of phyletic extinction rather than restricted distribution, and thus provides, in a negative way, evidence of strata of Namurian age.

Although each limestone in the Upper Limestone Group tends to have a characteristic fauna it is possible to recognise three faunal subzones.

a.) Faunal Assemblage 10A, includes the faunas of the Index and Lyoncross Limestones, and is characterised by Endothyra with a large number of chambers in the final whorl, low nodes and moderate axial rotation;

Paramillerella with low chamber counts, rather inflated quadrate chambers, and weak platform-like chomata. The great abundance of Endostaffella modica and the occurrence of Pseudoendothyra diaphana, Bradyina samarinaformis and Globivalvulina globulus, probably have only local significance within the subzone.

b.) Faunal Assemblage 10B, embraces the faunas of the Orchard and Calmy Limestones, and is characterised by small, tightly coiled, heavily chomate paramillerellids, Endothyra with few chambers, prominent hooks, and high axial rotation, and Bradyina with thick coarsely alveolar wall. Features of the subzone which are probably of local significance, subject to the variations in facies, are the abundance of Earlandia vulgaris and Archaediscus grandiculus in the Orchard Limestone, and Cerekia centrifuga, Novella minuta and associated forms in the upper Calmy position. This subzone is also marked by the first appearance in the Upper Limestone Group of the species Agathammina? robertsoni and Endostaffella inflata.

c.) Faunal Assemblage 10C, includes the faunas of the Plean and Castlecary Limestones, and

is distinguished by paramillerellids of markedly rectangular chamber form, high chamber count, and, in some cases, large diameter and high form ratio. Endothyra appears with prominent hooks, slight increase in the number of chambers present in the final whorl and low axial rotation. The appearance of the species Archaediscus karreriformis, Endothyra barbata, Endothyranopsis sphaerica, Globivalvulina parva, Glomospira dubilicata, Palaeonubecularia rustica, Paramillerella westerwoodensis, Tetrataxis triloba and Trochammina scotica are characteristic of this subzone but, in a number of instances, it is clear that the distribution of the forms is related to local conditions of environment, as reflected in the unusual algal facies of the Castlecary limestone.

EXPLANATION OF PLATE 27.

All figures X100 unless stated otherwise.

1-5. Gen et sp. nov. Cummings (1961 p.117).

1. sagittal section showing almost planispiral coil with slight deviations in coiling only in the early part of test. Note also constrictions of the tubular chamber producing irregular septation, X200. P.507. Calmy Limestone, Craigburn, Uddington.

2. axial section showing parallelism of sides, and slender chamber walls, P.508; Lyoncross Limestone, Rye Water, West of Drakemire, Dalry.

3,4. axial sections showing parallel sides and nearly planispiral coiling, P.509/1 & 2; Calmy Limestone, small stream near Castlecary Castle.

5. complete specimen immersed in clove oil seen in transmitted light and showing constrictions forming irregular septation of the test, P.510/1; Orchard Limestone, River Avon, Strutherhill.

6-11. Archaediscus krestovnikovi Rauser-Chernoussova.

6. axial section showing continuing irregularity in coiling and convex sides, P.511/1; Plean Limestone, Beoch Bore.

PLATE 27. - cont.

7. sagittal section showing irregularity in coiling continuing throughout growth. X200. P.512/1;

8. axial section showing variation in coiling and convex sides. X200. P.512/2.

Both from shales over Castlecary Limestone, Westerwood Quarry.

9. axial section P.513; Castlecary Limestone, Westerwood quarry.

10. axial section, P.514; Lyoncross Limestone, Overlee, Clarkston.

11. axial section, P.511/2; Plean Limestone, Beoch Bore.

12-14. Agathammina robertsoni (Brady).

12. showing fibrous wall structure comparable with Archaediscus, and coiling about an elongate axis. X200. P.515; Castlecary Limestone, Westerwood Quarry.

13,14 sections at right angles to elongate coiling and showing the sigmoid path of the whorls, P.516/1 & 2; thin limestone above Calmy Limestone, Craigburn, Uddington.

PLATE 27. - cont.

17-24. *Archaediscus* cf. *grandiculus* Schlykova.

17. section in plane of maximum diameter, P.517/1;

18. section in plane of minimum diameter, P.517/2;

Both from shales over Orchard Limestone, River Avon, Strutherhill.

19. oblique section, P.518/1; River Nethan, Auchlochan House.

20. oblique section, P.519; Castlecary Limestone, Levenseat Quarry & Mine.

21. oblique section, P.520; Lyoncross Limestone, Craigburn, Uddington.

22,24 oblique sections, P.521/1 and P.521/2; Orchard Limestion, Poniel Water, Coalburn.

23. Oblique section, P.518/2, River Nethan, Auchlochan House.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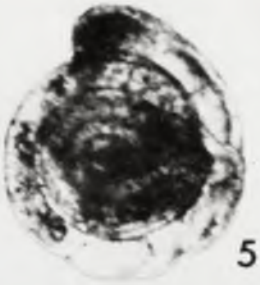
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EXPLANATION OF PLATE 28.

All figures X100 unless stated otherwise.

1,2. *Palaeonubecularia rustica* Reitlinger.

1. encrusting agglutinate tubes on shell fragments. X50. P.522/1;
2. growing on, and intimately associated with *Girvanella* sp. nov. X50. P.522/2;

from Castlecary Limestone, Westerwood Quarry.

3-8. *Cornuspira intermedia* (Waters).

3,5. sagittal sections showing slender tube and slow expansion of the spiral. P.523/1 and P.523/2;

4,6. axial sections, showing small size and strongly complanate character of the test. P.523/3 and 523/4;

All from Castlecary Limestone, Westerwood Quarry.

7. sagittal section, P.524; Calmy Limestone, Diddup Burn, Dalry.
8. as fig.6, X250.

9-15. *Cepekia centrifuga* (Brady).

9. axial section, P.525; Calmy Limestone, Monkcastle Burn, Dalry.
10. sagittal section showing constrictions in chambers indicating the positions at which

PLATE 28. - cont.

the tube becomes incipiently rectilinear. P.526; Calmy Limestone, Loans Quarry, Bembo Burn, Dalry.

11. sagittal section showing series of pseudo-chambers, P.527/1;

12. axial section, P.527/2;

13,15 sagittal sections, P.527/3 and P.527/4;

All from thin limestones over Calmy Limestone, River Nethan, Auchlochan House.

14. axial section, P.528; from thin limestone band over Calmy Limestone, Craigburn, Uddington.

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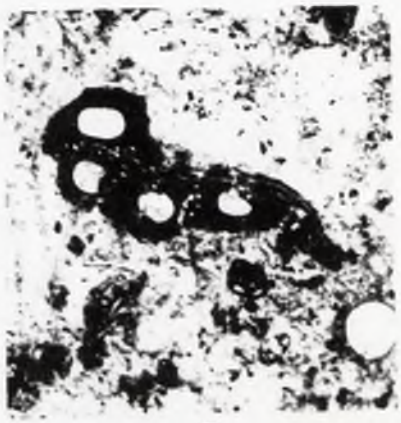

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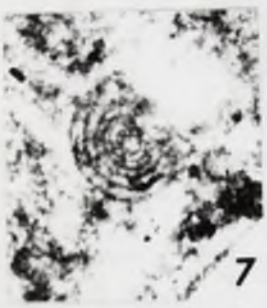

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EXPLANATION OF PLATE 29.

All figures X100 unless stated otherwise.

1-4. Glomospira? dubilicata Lipina.

1-4 sections showing the irregular streptospiral mode of coiling and dark homogeneous, finely granular, calcareous wall, P.529/1-4; from Castlecary Limestone, Westerwood Quarry.

5-8,11. Calcivertella sp.

5, longitudinal section, P.530;

6. section showing circular internal cavity without evidence of structure to which it was attached, P.531;

7,8 & 11 show similar structures, P.532, 533 and 534;

All from Castlecary Limestone, Westerwood Quarry.

9. Calcivertella sp.

longitudinal section in plane of coiling, P.535; Index Limestone, Poniel Water, Coalburn.

10. Calcivertella cf. adhaerens Cushman & Waters.

section in the plane of coiling, P.536; Lyoncross Limestone, Craigburn, Uddington.

PLATE 29. - cont.

12-14. Earlandia pulchra Cummings.

12. longitudinal section, P.357; Index Limestone, Poniel Water, Coalburn.

13,14 longitudinal sections showing proloculum and simple tubular second chamber, P.538/1 and 2; Castlecary Limestone, Westerwood Quarry.

15-18. Earlandia vulgaris (Rauser - Chernoussova & Reitlinger.).

15. longitudinal section showing coarsely granular wall, constriction of tube, illustrating periodic growth, but without septation, P.539/1;

16. longitudinal section showing changes in alignment of non-septate chambers, P.539/2. X50.

Both from Orchard Limestone, River Nethan,, Auchlochan House.

17,18 sections showing large prolocula; Orchard Limestone, Bilston Burn, Penicuik and Garpel Water, Craigburn; P.540 & P.541.

PLATE 29. - cont.

19,20. Tuberitina maljavkini Mikhailov.
sections showing single globose chamber with slender wall and concave disc of attachment, P.541/1 and 2; Castlecary Limestone, Westerwood Quarry.


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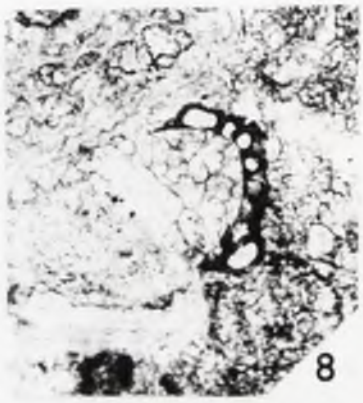
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EXPLANATION OF PLATE 30.

All figures X100.

1. Calcivertella? sp.
section in the plane of coiling viewed in reflected light; from excavated limestone slice, P.543; Lyoncross Limestone, Craigburn, Uddington.

2-5. Calcivertella cf. adhaerens Cushman & Waters.
2-4. sections excavated from limestone slices and showing variation in form of the test produced by the irregular periodic wind-:ing of the tubular chamber, P.544/1-3; Lyoncross Limestone, Craigburn, Uddington.
5. a similar section, P.545; Lyoncross Limestone, Whitecraigs, Renfrewshire.

6. Calcitornella cf. heathi Cushman & Waters.
an excavated section showing an enrolled early stage and zig-zag later stages, P.546: Lyoncross Limestone, Whitecraigs, Renfrewshire.

7-9. Calcivertella cf. adhaerens Cushman & Waters.
7. free specimen showing zig-zag early coils partly enrolled by final portion of tube, P.547/1;

PLATE 30. - cont.

8,9. opposite views of specimen showing the zig-zag early part of the tube partly enrolled by later stages, P.547/2.
All from shales over Orchard Limestone, River Avon, Strutherhill.

10,11. Gen et sp. nov. Cummings (1961 p.117). lateral views of this small archaediscid to show constrictions of tubular chamber, and near planispiral coiling, P.510/1 and 2. (cf. Plate 27, fig.5); Orchard Limestone, River Avon, Strutherhill.

12. Agathammina robertsoni (Brady). simple tubular chamber coiled about elongate axis, P.516/3; thin limestone above Calmy Limestone, Craigburn, Uddington.

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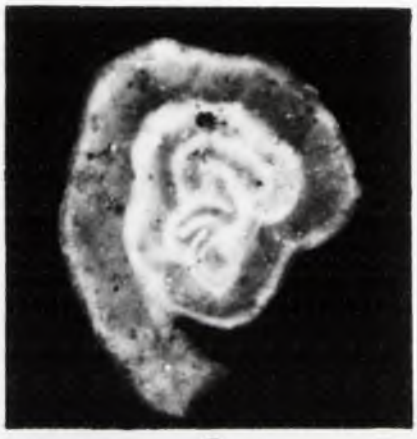

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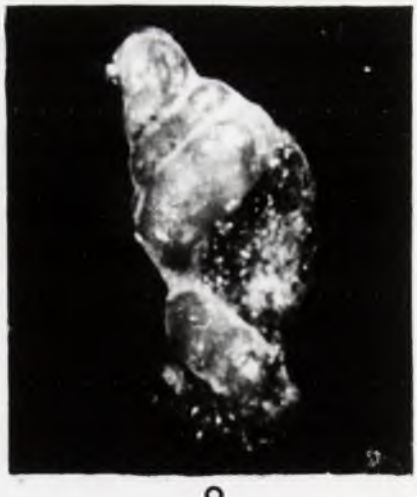

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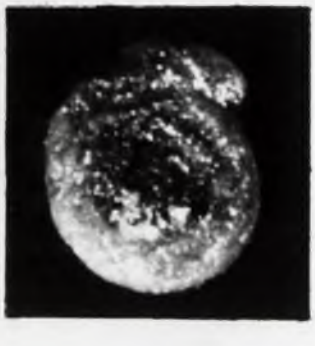

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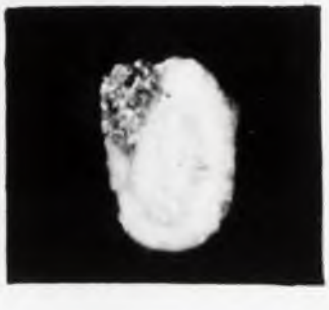

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EXPLANATION OF PLATE 31.

All figures X100 unless stated otherwise.

1-3,5. *Cepekia centrifuga* (Brady).
lateral views showing angularity of test, marking positions of incipient rectilinear growth and showing varying development of final rectilinear stage, P.547/1-4; thin limestone over Calmy Limestone, Craigburn, Uddington.

4. *Novella minuta* sp. nov.
lateral view of holotype in reflected light, P.440/4, (cf. Plate 11, fig.24); from shales over Orchard Limestone, River Avon, Strutherhill.

6,7. *Endostaffella modica* sp. nov.
6. apertural view showing evolute coiling, but note evidence of axial rotation in asymmetry of last chamber and form of final whorl.
7. lateral view of same specimen, P.548;
both from shales over Lyoncross Limestone, Whitecraigs, Renfrewshire.

8,9. *Earlandia pulchra* Cummings.
specimens showing proloculum and broken tubular second chamber. X50. P.549/1,2; from thin limestone above Plean Limestone, Craigburn,

PLATE 31. - cont.

10. Earlandia vulgaris (Rauser-Chernoussova & Reitlinger).
specimen showing large proloculum and expanding tubular second chamber. X50, P.550; shales over Orchard Limestone, River Avon, Strutherhill.

11,13. Lugtonia elongata Cummings.
11. lateral view showing overlapping series of chambers, P.487/2;
13. lateral view of large specimen; the smallest chamber probably is not the proloculum, P.487/3;
from shales over Orchard Limestone, River Avon, Strutherhill.

12. Lugtonia minima Cummings.
lateral view showing compressed chambers, P.488; shales over Orchard Limestone, River Avon, Strutherhill.

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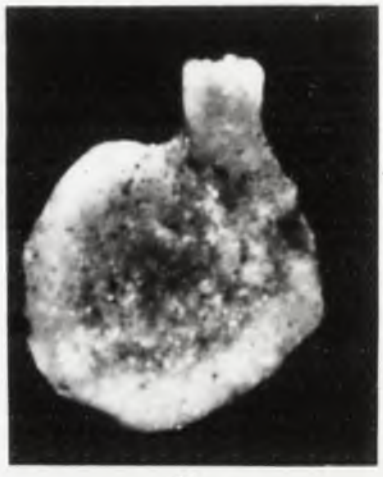

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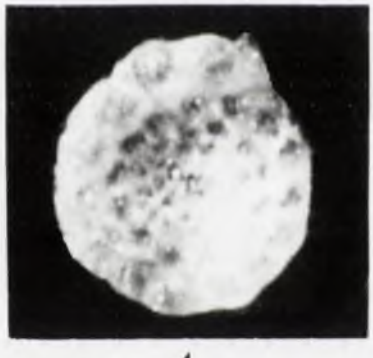

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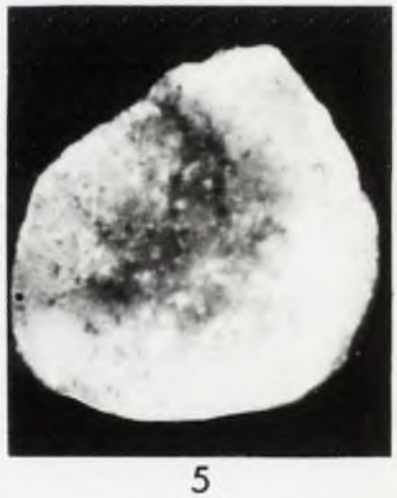

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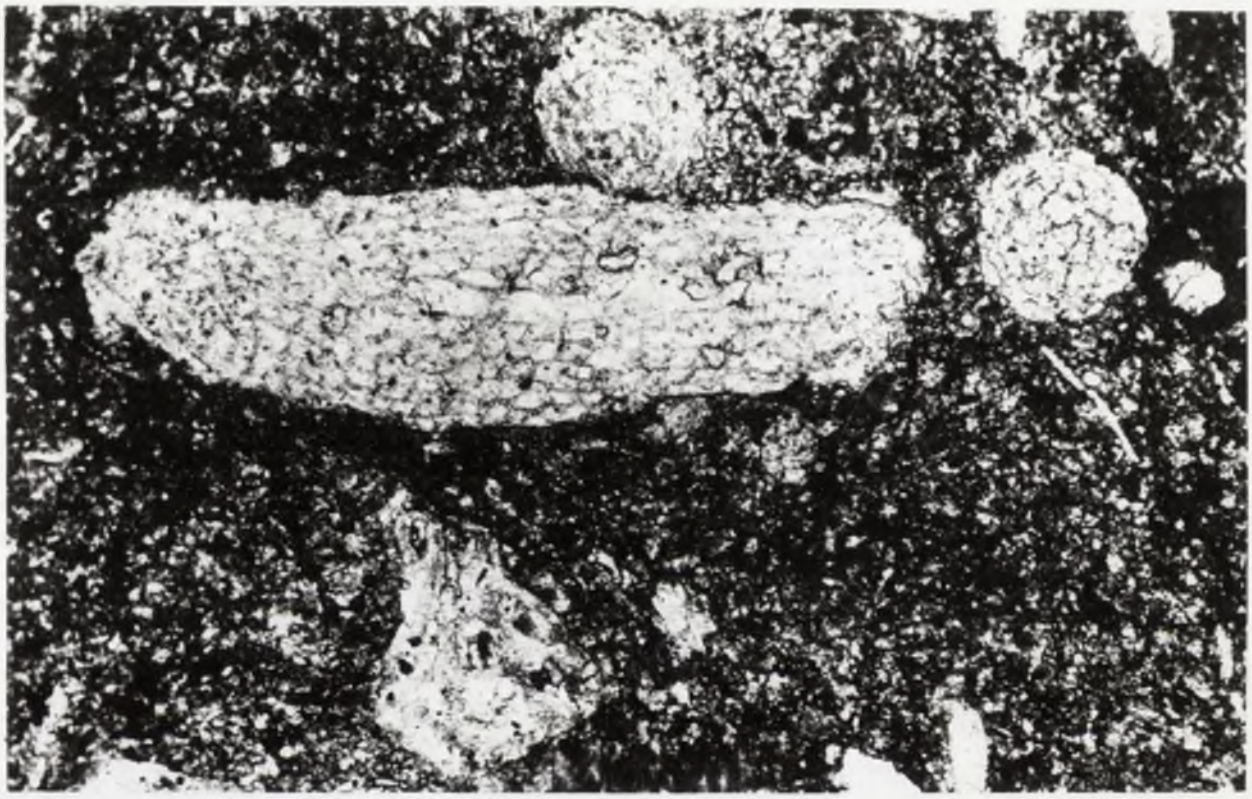
EXPLANATION OF PLATE 32.

All figures X100.

1. *Stacheoides* sp.
random sections showing sheet-like growth of chamberlets in longitudinal section and concentric arrangement in transverse sections. Note also fragment of *Aujgalia* sp. in lower centre portion of figure, P.551; Index Limestone, Kerse Farm, Kilbirnie.

2,3. *Stacheoides* sp.
longitudinal and transverse sections of a rather thicker walled form encrusting on brachiopod spines, P.552/1 and 2; from Lyoncross Limestone, Craigburn, Uddington.



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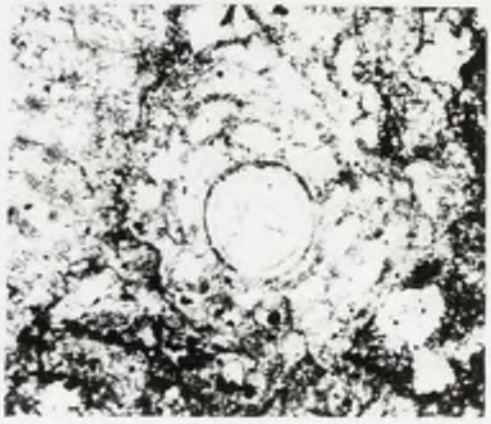

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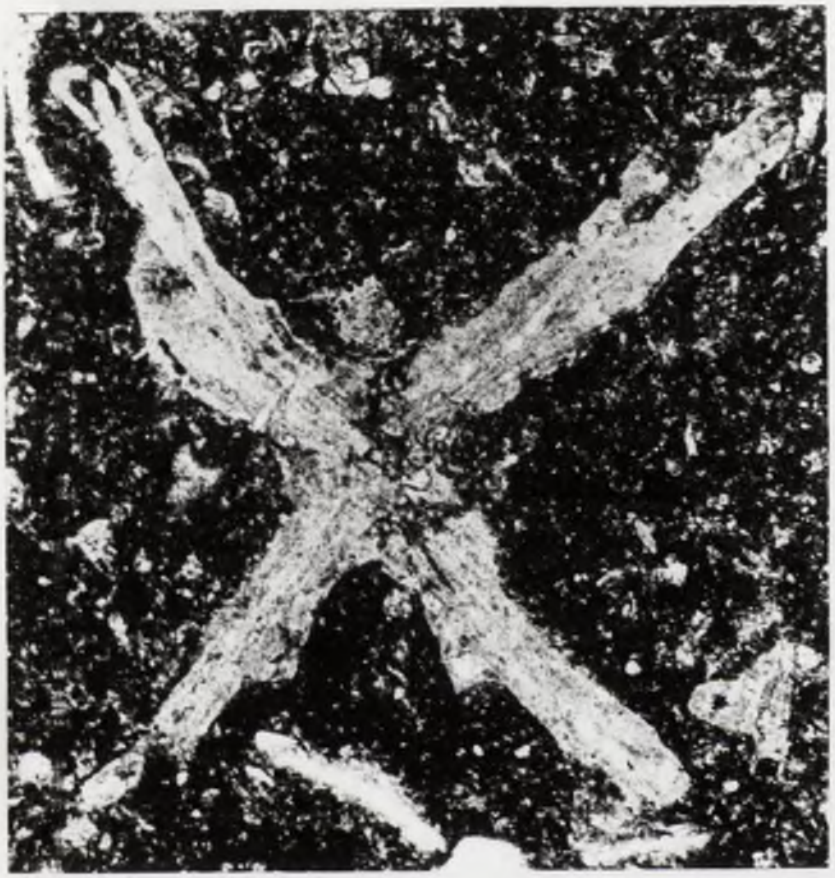
EXPLANATION OF PLATE 33.

1-3. *Aoujgalia* sp. nov.

1. random thin section showing typical cruciform development of the chambers from the point of attachment. X100. P.552/1.

2,3. excavated sections in limestone by reflected light, showing central complex of more irregular chamberlets round point of attachment, and rectilinear series of interconnected chamberlets producing branches. X50. P.532/2 and 3.

All from Lyoncross Limestone, Whitecraigs.



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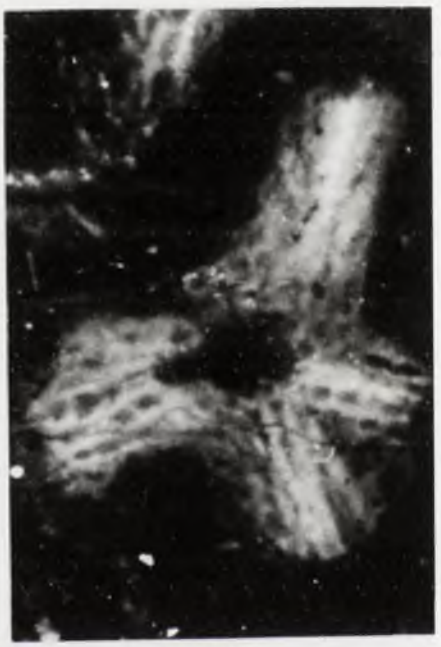

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EXPLANATION OF PLATE 54.

1. Palaeotextulariid fragment showing small archaediscid in the wall, X100, P.553; Index Limestone, Poniel Water, Coalburn.

2. Palaeotextulariid fragment showing adventitious material incorporated in the wall, including tests of Endostaffella sp. and Calcivertella sp. X100, P.554; Orchard Limestone, Poniel Water, Coalburn.

3. Palaeotextulariid fragment with test of Endostaffella sp. incorporated in the wall, P.555; Orchard Limestone, Poniel Water, Coalburn.

4,7. Climacammina sp.

4. parallel axial section revealing evidence of porous structure in palaeotextulariid wall. The wall, heavily impregnated by fine pyrite dust, is easily distinguishable from the clear calcite in the pores. Oblique transverse sections of the pores are well seen on the right side of the last chamber, X50.

7. the final chamber in fig.4, X200. P.554; Lyoncross Limestone, Garpel Water, Muirkirk.

PLATE 34. - cont.

5,6. Palaeotextulariids showing unusual preservation of wall structure.

5. syntaxial replacement of the outer granular layer of the wall by enlargement of the inner fibrous buttresses, X100, P.555; Castlecary Limestone, Westerwood Quarry.

6. replacement of the original wall structure by coarse dolomite, X100, P.556; Castlecary Limestone, Joppa.

8. Palaeotextulariid fragment showing wall with abundant incorporated calcareous debris including two calcispheres, X200, P.557; Orchard Limestone, Lugton Water, Montgreenan.


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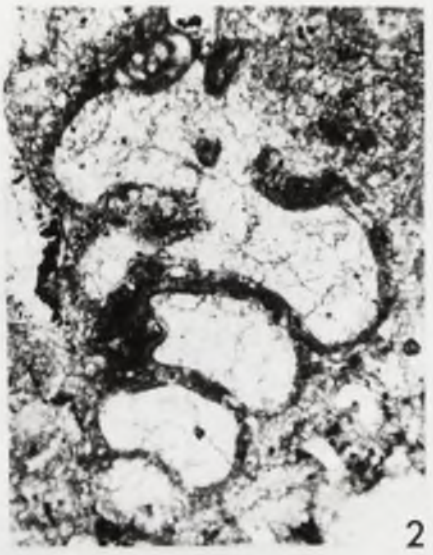
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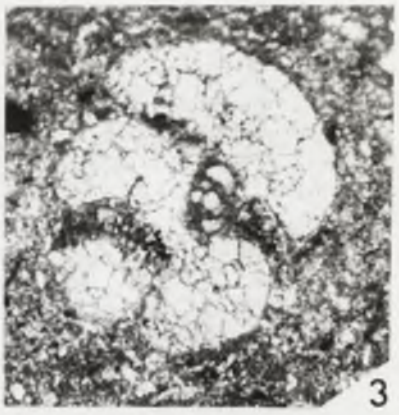
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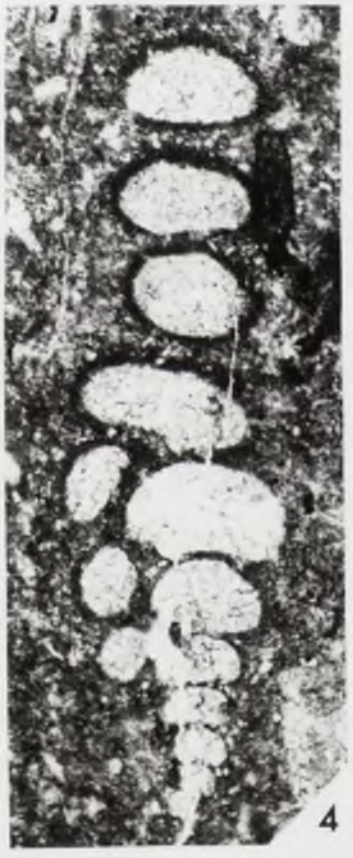
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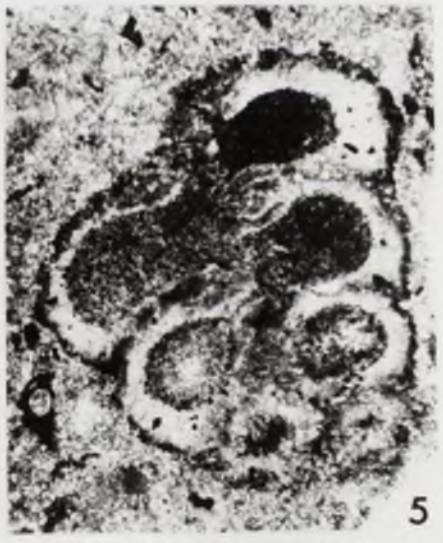
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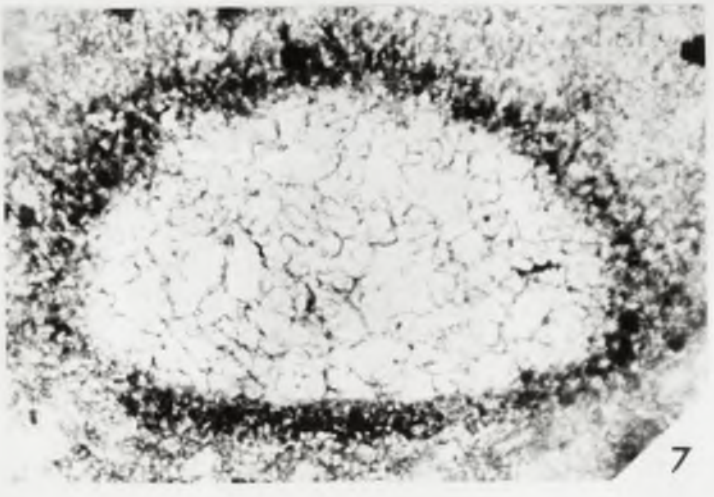
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EXPLANATION OF PLATE 35.

All figures X50.

1,2. Climacammina prisca Lipina.
oblique sections, P.558/1,2; Index Limestone, Auldhouse Burn, Muirkirk.

3. Climacammina bradyi (Moeller).
longitudinal section showing the proloculum, P.559; Index Limestone, Poniel Water, Coalburn.

4. Climacammina antiqua (Brady).
oblique longitudinal section, P.560; Lyoncross Limestone, Craigburn, Uddington.

5. Climacammina cf. supraparva Cummings.
oblique section, P.561; Calmy Limestone, Diddup Burn, Dalry.

6. Climacammina cf. bradyi (Moeller).
oblique section, P.562; Orchard Limestone, Poniel Water, Coalburn.

7. Climacammina sp.
section in X-nicols showing infilling of chambers by finely granular phosphate, P.563; shales over Orchard Limestone, Poniel Water, Coalburn.

PLATE 35. - cont.

8-10. Climacammina supraparva Cummings.

8-9. oblique sections P.564/1 and 2;

10. longitudinal section, P.564/3;

from Castlecary Limestone, Westerwood Quarry.

11. Climacammina cf. antiqua (Brady).

oblique section, P.565; Castlecary Limestone, Westerwood Quarry.


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